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The Neural Substrates of Object Individuation

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Abstract

Despite the constant influx of visual information, observers are nonetheless able to segment this input into discrete objects and events. The perceptual system does so on the basis of spatial and temporal properties, thus allowing one to keep track of visual objects as they move to different locations across time. This process of *object individuation* is integral for visual awareness; when it is disrupted, stimuli are no longer perceived. Behavioural studies that have investigated object individuation in temporal and spatial domains converge on the idea that object individuation is a capacity-limited process that gates which items proceed for further analysis. Although there has been considerable theoretical and behavioural work on object individuation, we know relatively little about its neural substrates. The experiments in this thesis investigate the brain regions that support object individuation across multiple episodic contexts and processing stages, characterise its capacity limits and relationship to identification, and isolate the stage of processing at which individuation arises.

Chapter 2 describes a functional magnetic resonance imaging (fMRI) study that isolated the neural bases of temporal individuation during perception, and the consequences that arise when its processing limit is reached (repetition blindness, RB). RB is a rapid serial visual presentation phenomenon characterised by reduced performance on trials with a target repetition compared with those in which the two targets have different identities (non-repetition trials). This failure of perceptual consciousness is thought to reflect a capacity limit of temporal individuation. I first verified that my RB paradigm elicited the standard behavioural effect (Experiment 1) and was specific to the temporal limits of individuation, rather than identification (Experiment 2). Using fMRI (Experiment 3), I found that multivariate patterns of blood-oxygen-level-dependent (BOLD) activity across a large number of occipital, parietal and frontal regions could discriminate between trials in which a repetition was correctly reported (a demanding individuation scenario), compared with correct non-repetition trials (a relatively easy individuation scenario). Consistent with current models of consciousness, and contrary to existing work on spatial individuation at the level of memory encoding, these findings suggest that temporal individuation is supported by a distributed set of brain regions. In terms of RB itself, I found greater activity in the left premotor cortex for incorrect versus correct repetition trials. This result suggests that the left premotor region is critical for the processing limitations that give rise to RB.

In Chapter 3, I tested whether object individuation and identification can be dissociated in the brain at the level of visual short-term memory (VSTM) encoding and

beyond, as proposed in the neural object file theory. Participants completed a delayed VSTM task in which they had to remember the identity and spatial locations of one object, four identical objects or four different objects. To isolate object individuation regions, BOLD activity was compared between one object and four identical objects. By contrast, to identify object identification regions, BOLD activity was contrasted between four identical objects and four different objects. Across univariate and multivariate analyses, I found brain regions that were specific to individuation or identification processes, and others that were common between the two. These findings challenge the neural object file theory, and instead suggest that object individuation and identification processes have distributed and overlapping neural substrates.

The aim of the experiments reported in Chapter 4 was to characterise the timecourse of object individuation for attended and unattended objects, and determine the extent to which this operation draws on early sensory cortices. Previous event-related potential (ERP) studies were unable to show definitive evidence of object individuation at early perceptual stages of analysis, because the paradigms in these studies confounded manipulations of individuation load (i.e., number of targets) with low-level visual features (e.g., luminance). I first developed a novel enumeration paradigm involving items defined by illusory contours, which held all physical properties constant across conditions (Experiment 1), and then used electroencephalography (EEG) to investigate the timecourse of object individuation for attended and unattended stimuli (Experiment 2). Both P1 (100-140 ms) and N2 (185-250 ms) amplitudes increased with the number of attended targets, but the number of unattended non-targets only modulated the N2. An fMRI study (Experiment 3) showed that early visual cortex (including V2) was sensitive to individuation load, which I hypothesised might underpin the observed P1 effect. These findings demonstrated that task-relevant individuation occurs at a relatively early stage of visual information processing, and voluntary spatial attention modulates the timecourse of this operation.

Taken together, the experiments reported in this thesis offer novel insights into our understanding of the neural underpinnings of object individuation across various stages of processing. These findings have implications for current theoretical accounts of object individuation and its associated processes in the brain, and contribute to models of how individuation should be operationalised as a construct.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

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Publications during candidature

Peer-Reviewed Papers:

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Naughtin, C. K., Tamber-Rosenau, B. J., & Dux, P. E. (2013). The neural basis of temporal individuation and its capacity limits in the human brain. *Journal of Neurophysiology, 111*(3), 499-512. doi: 10.1152/jn.00534.2013.

Bayliss, A. P., Murphy, E., **Naughtin, C. K.,** Kritikos, A., Schilbach, L., & Becker, S. I. (2013). 'Gaze leading': Initiating simulated joint attention influences eye movements and choice behaviour. *Journal of Experimental Psychology: General*, *142*(1), 76-92. doi: 10.1037/a0029286

Bayliss, A. P.*, **Naughtin, C. K.***, Lipp, O. V., Kritikos, A., Dux, P. E. (2012). Make a lasting impression: The neural consequences of reencountering people who emote inappropriately. *Psychophysiology*, *49*(12), 1571-1578. doi: 10.1111/j.1469-8986.2012.01481.x
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Naughtin, C. K & Dux, P. E. (2011). A neural dissociation of repetition blindness and repetition suppression. 2nd UQ Centre for Perception and Cognitive Neuroscience Workshop, Brisbane, Australia.

Publications included in this thesis

This thesis contains three empirical chapters (Chapters 2, 3 and 4) that contain studies have been published or submitted at a peer-review outlet. These studies are contextualised with a General Introduction (Chapter 1) and a General Discussion (Chapter 5). Below I list the citation and contributions for each of the empirical articles.

Naughtin, C. K., Tamber-Rosenau, B. J., & Dux, P. E. (2013). The neural basis of temporal individuation and its capacity limits in the human brain. *Journal of Neurophysiology, 111*(3), 499-512. doi: 10.1152/jn.00534.2013. Incorporated in Chapter 2.

Contributor	Statement of contribution
Claire K. Naughtin	Conceptualised & designed experiments (60%) Data collection, analysis & interpretation (60%)

	Wrote the paper (60%)
Benjamin J. Tamber-Rosenau	Data collection, analysis & interpretation (20%) Wrote the paper (10%)
Paul E. Dux	Conceptualised & designed experiments (40%) Data collection, analysis & interpretation (20%) Wrote the paper (30%)

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Claire K. Naughtin	Conceptualised & designed experiments (60%) Data collection, analysis & interpretation (60%) Wrote the paper (60%)
Jason B. Mattingley	Conceptualised & designed experiments (20%) Data collection, analysis & interpretation (20%) Wrote the paper (20%)
Paul E. Dux	Conceptualised & designed experiments (20%) Data collection, analysis & interpretation (20%) Wrote the paper (20%)

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Contributor	**Statement of contribution**
Claire K. Naughtin	Conceptualised & designed experiments (60%) Data collection, analysis & interpretation (60%) Wrote the paper (60%)
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Paul E. Dux	Conceptualised & designed experiments (20%)

	Data collection, analysis & interpretation (20%) Wrote the paper (20%)

Contributions by others to the thesis

Paul Dux and Jason Mattingley were key contributors to this thesis and were involved in the conceptualisation, design and interpretation of experiments, the development of the candidate's research skills and proof-reading of manuscripts and the thesis as a whole. Benjamin Tamber-Rosenau was integral to imaging data analysis in Chapter 2. Aiman Al Najjar, Mark Strudrick, Daniel Stjepanovic and Zoie Nott (MRI operators) assisted with the imaging data collection in Chapters 2, 3 and 4. Rebecca King, Amy Taylor and Luke Hearne (research assistants) also assisted in behavioural data collection on Chapter 2, 3 and 4. Oscar Jacoby assisted with data analysis on Chapter 4.

Statement of parts of the thesis submitted to qualify for the award of another degree

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Keywords

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THE NEURAL SUBSTRATES OF OBJECT INDIVIDUATION

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List of Abbreviations Used in Thesis

3D: Three-dimensional

4I: Four identical

4D: Four different

A1: Primary auditory cortex

AB: Attentional blink

ACC: Anterior cingulate cortex

AC-PC: Anterior commissure-posterior commissure

ANOVA: Analysis of variance

ARC: Australian Research Council

BA: Brodmann area

Bi: Bilateral

BESA: Brain electrical source acquisition

BOLD: Blood oxygen level dependent

C1: First critical item

C2: Second critical item

CR: Correct rejection

DLPFC: Dorsal lateral prefrontal cortex

EEG: Electroencephalography

EOG: Electrooculogram

ERP: Event-related potential

FA: False alarm

FDR: False discovery rate

fMRI: Functional magnetic resonance imaging

FOV: Field of view

GRE EPI: Gradient-echo echo planar imaging

IFJ: Inferior frontal junction

IPS: Intra-parietal sulcus (iIPS, inferior; sIPS, superior)

ITI: Inter-trial interval

L: Left

LOC: Lateral occipital complex

MPRAGE: Magnetization prepared rapid gradient echo

MVPA: multi-voxel pattern analysis

N1: First negative component

N2: Second negative component

N2pc: Lateralised N2 component

P1: First positive component

PMC: Premotor cortex

PPA: Parahippocampal place area

R: Right

RB: Repetition blindness

ROI: Region of interest

RT: Reaction time

RSVP: Rapid serial visual presentation

SD: Standard deviation

SMFC: Superior medial frontal cortex

SPL: Superior parietal lobule

SRI: Science of Learning Research Centre

TE: Echo time

TR: Repetition time

V1: Primary visual cortex

V2: Secondary visual cortex

V3-V5: Extrastriate visual cortex

VSTM: Visual short-term memory

CHAPTER 1: INTRODUCTION

The ability to separately encode information about an object's spatiotemporal location and its features is vital for visual perception (Marr, 1982). Schneider (1969) was the first to make this distinction between 'what' and 'where' processing in vision, and it has been maintained even if the original neural mechanisms he proposed for these operations have not. If one fails to register the correct position of a particular feature, severe perceptual errors can arise (e.g., misjudging the location of a hazard when crossing the street). Such misperceptions are apparent in *illusory conjunctions*, where a specific feature of a stimulus (e.g., its colour) is mistakenly paired with another feature (e.g., its shape) that is not present in the current stimulus, but is part of another item at a different location (Treisman & Gelade, 1980). For example, in a display containing a red 'X' and a green 'O,' the items could be incorrectly perceived as a green 'X' and a red 'O' (Treisman & Schmidt, 1982; Treisman & Gelade, 1980). Observers can also show impairments in their ability to assign the same attribute to separate stimuli that appear in different points in time or space (Kanwisher, 1987; Mozer, 1989; Park & Kanwisher, 1994). The idea that object features are bound to a specific spatial location or time point is only useful in the case of static stimuli, however, because otherwise a new object would be perceived each time the stimulus moves or is momentarily occluded in the visual scene. Instead, the visual system must rely on some sort of mechanism to index, or individuate, an object as a distinct, continuous representation across changes in time and space.

In this chapter, I outline recent theoretical and empirical work on two processes that are critical for the encoding of spatiotemporal and identity information about visual objects, namely, *object individuation* and *object identification*. I also discuss accounts concerning how this information is linked to create integrated representations. In addition, I present cognitive-neuroscientific models that have been introduced to characterise how the human brain differentially processes information about what an object is and where/when it appears. Finally, I outline several outstanding questions in the field. For example, how is the ability to individuate objects across time reflected in the brain? What neural consequences arise when this process reaches its capacity limit? Do individuation and identification processes overlap in the brain? Does object individuation draw on selective attention mechanisms? And, at what stage of information processing does individuation take place? In the following chapters, I present empirical investigations that employ a range of behavioural and neurophysiological approaches to address these questions.

Processing What, Where and When in Vision

Several theoretical models have proposed that visual attributes are organised into abstract object representations that are independent of where the object appears. In his FINST (or 'fingers of instantiation') theory of visual indexing, Pylyshyn (1989, 1994; 2001) argued for a pre-attentive mechanism that allows the visual system to individuate a particular object as a perceptual entity that is distinct from other objects. The notion of FINSTs is analogous to pointing at an object in the external environment with one's finger. In this scenario, one is able to register the presence of an object and update its specific spatial location if it moves, but one cannot glean any information about the object's attributes. In this sense, FINSTs can be described as 'sticky'; they allow an observer to track an object, and recognise when the same object persists in a visual scene, even if it changes its spatial and, therefore, retinal location (Pylyshyn & Storm, 1988). Pylyshyn proposed that individuating an object occurs prior to, and without the need for, the extraction of featural information that is necessary to identify the object. A limited set of FINSTs can be created in parallel for multiple specific features of an object – or to a cluster of features – and this assignment is likely to be driven by bottom-up, stimulus-driven features caused by a sudden onset (Jonides & Yantis, 1988; Remington, Johnston, & Yantis, 1992) or shape change (Miller, 1989; Theeuwes, 1991). FINSTs can also act as a pointer for guiding top-down processes like focal attention (Pylyshyn, 1989; Pylyshyn, 2001).

Pylyshyn and Storm (1988) provided an empirical demonstration of the FINST mechanism. They reasoned that, if FINSTs are indexed independently of any analysis of identity information, observers should be able to track a subset of items even if they are identical to non-tracked items. Specifically, Pylyshyn and Storm (1988) tested whether observers could track several moving targets embedded in a display with distractor items, where all items were identical in appearance (see Figure 1). To complete this task, observers had to track the targets over time, but could not rely purely on identity information (as this was constant across all items) or the specific memory of a prior spatial location (unless this was updated at a sufficient frequency). In the experiment, a static display consisting of ten items was initially presented, in which one to five of the items flashed. The flashing items denoted the targets observers were to keep track of, and the remaining stimuli were distractors. All stimuli then began moving around the visual display in random directions, during which time a solid white square would briefly replace one of the target or distractor items (there were four flashes in total with only a single target event). Observers were required to make a speeded button press when the flash occurred

over a target item (this paradigm is now know as *multiple object tracking*; Scholl, Pylyshyn, & Feldman, 2001). Although performance declined with increasing number of targets, observers were still able to track up to four or five items with a high level of accuracy (approximately 85%). This finding suggests observers are able to simultaneously individuate and track multiple objects on the basis of their spatiotemporal properties, rather than their identity, and that this process is resource-limited.

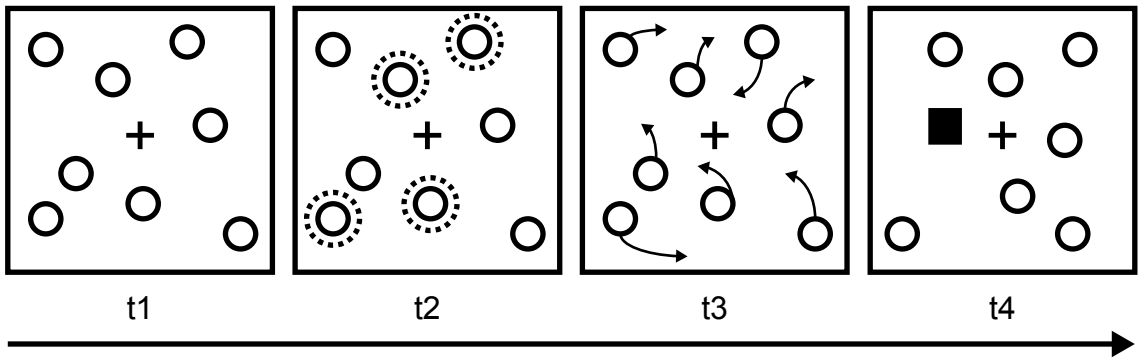

Figure 1. Schematic representation of a standard multiple object tracking paradigm. Each trial begins with a static display of items (t1), some of which flash (t2), and these items are defined as targets (flashing items are denoted here by a circular dotted line). All items then begin moving around the display in a random fashion (t3). During this period, a given item can briefly change to a solid white square (shown in black here), and if this item is a target, participants are instructed to make a speeded button press (t4). This figure was reproduced from Pylyshyn (2001) with permission from Elsevier Limited.

The notion of a pre-attentive mechanism that individuates and indexes multiple objects in a visual scene was also a key component of the object file framework introduced by Kahneman, Treisman, and Gibbs (1992). This theory accounts for how objects are initially selected and then processed up to awareness. The term *object files* refers to a temporary episodic representation (token), which is distinct from stored long-term memory representations that are used to determine an object's identity (type; Kahneman & Treisman, 1984). Each object file contains information about the object's spatial location at a particular time point and any additional sensory information that has been acquired about that object. The contents of the object file may include featural information, but an object file is created and maintained predominantly on the basis of its spatiotemporal properties. Object files can be created for groups of objects (e.g., a bowl of fruit) or a single object (e.g., an apple), and the level at which objects are defined depends on top-

down factors, such as attention (LaBerge, 1983; Navon, 1977), or bottom-up factors, such as grouping (Baylis & Driver, 1992). To recognise an object, sensory information contained in the object file is compared against that stored in long-term memory. If there is a match between the current object file and a stored representation, recognition occurs and relevant identity information and its associated characteristics (e.g., the appropriate behavioural response) are added to the object file.

The contents of an object file are updated whenever its sensory characteristics change, such as when the object moves to a different spatial location. If the new sensory information cannot be matched to an existing file, a new one is created. Kahneman, Treisman, and Gibbs (1992) refer to three separate operations that are necessary for maintaining an object file. First, a *correspondence* operation determines whether an object is new or is a previously seen object that has changed location. Second, a *reviewing* process occurs in which previous sensory information about an object that is no longer visible is retrieved. Third, in the *impletion* operation, both current and reviewed information are used to create a percept that links the two. When the current and reviewed information from the reviewing phase match, the two objects are seen as corresponding to the same object at two separate points in time. If there is no match, there will be no correspondence between the two objects and the information associated with each will be assigned to separate object files.

Kahneman et al. (1992) introduced the object reviewing paradigm to demonstrate the role of object files in maintaining the percept of a single object across changes in time and space (see Figure 2). In the preview phase of this task, two or more letters are presented in separate placeholder boxes that appear at distinct locations. Then, during the target phase, only a single letter appears in one of the placeholders. The target letter is manipulated to be the letter that appeared in that same box at preview, in a different box at preview, or a novel letter that did not appear in either of the preview boxes. Observers are typically faster to identify the target letter when it is the same letter that appeared in the corresponding box at preview than when it was presented in a different box, or was absent from the display. This *object-specific preview advantage* effect is thought to indicate that the target is processed more efficiently when its stimulus information is retrieved from the same object file created at preview than when an entirely new object file must be created or substantially updated. Object files are therefore another potential mechanism by which stimuli can be individuated in a visual scene and maintained across changes in time, space and appearance. Although there are differences in the types of theoretical problems they aim to address (for a discussion, see Kahneman et al., 1992), both FINSTs and

object files nevertheless assume a stage of processing in which an object can be individuated as a distinct entity, and that this phase can proceed independently of any sort of featural analysis.

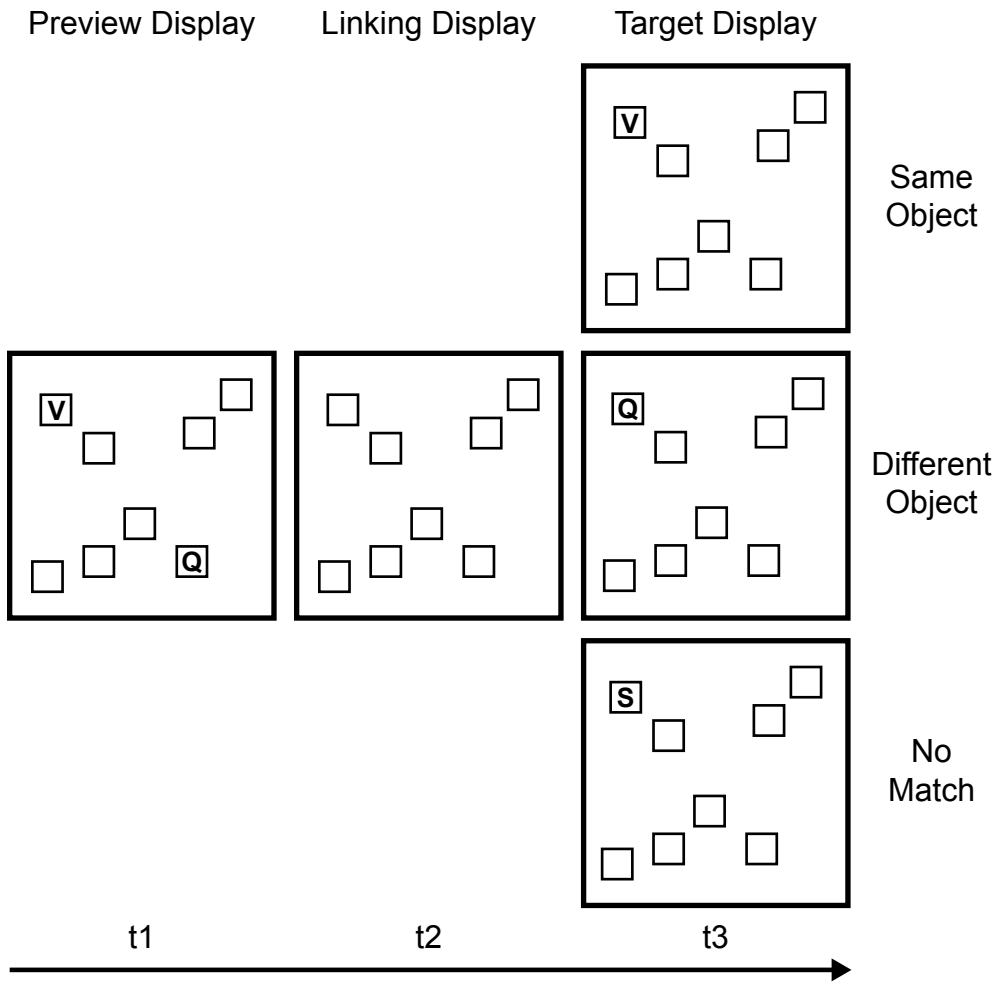

Figure 2. Schematic representation of a standard object reviewing paradigm.
A preview display first appears with a series of placeholders, two of which contain sample items (t1). Participants' task is to remember the identities and locations of these items. Following a linking phase (t2), a single target item appears in one of the placeholders (t3). The target item matches the identity and location of one of the preview items (same object), matches the identity of the other preview item that appeared at a different location (different object), or matches neither of the previewed items (no match). This figure was reproduced from Kahneman et al. (1992) with permission from Elsevier Limited.

Processing What, Where and When in the Brain

The theoretical accounts and behavioural evidence discussed thus far support the notion of separate individuation and identification processes in visual perception. A similar

distinction has been made in the terms of how, what, where and when information is represented and processed in the brain. Based on electrophysiological, anatomical and behavioural evidence, Ungerleider and Mishkin (1982) proposed that two anatomically distinct neural pathways are responsible for many aspects of visual perception: An occipitotemporal ('ventral') pathway responsible for object identification, or processing 'what' information, and an occipitoparietal ('dorsal') pathway that underpins spatial perception, or the analysis of 'where' information. These two streams receive independent outputs from the striate cortex. Information for the ventral stream is projected to the inferotemporal cortex, whereas the dorsal stream projects to the posterior parietal cortex. The key evidence in support of these two functionally distinct pathways comes from lesion studies (e.g., Gross, 1973; Mishkin, 1966; Mishkin & Ungerleider, 1982; Pohl, 1973). Mishkin (1966) found that monkeys with a lesion to the striate cortex in one hemisphere and an inferotemporal lesion in the opposite hemisphere could still perform well on a pattern discrimination task. If the corpus callosum was severed to disrupt the single remaining striatal-inferotemporal connection, however, task performance dropped to chance, implicating this pathway in object perception. An analogous cross-lesion dissection study was conducted by Mishkin and Ungerleider (1982) to explore the functional role of striatal-parietal connections. These authors found decrements in performance on a landmark discrimination task following an initial lesion to a single contralateral striatal-parietal connection and the subsequent lesion to the connecting corpus callosum region, suggesting that this cortical pathway is necessary for spatial perception.

Human lesion studies provided converging evidence for the functional dissociation between ventral and dorsal visual processing pathways for identity and location information, respectively. For instance, patients who develop visual agnosia as a result of damage to areas including the occipitotemporal region, struggle to recognise or discriminate a range of simple visual stimuli (e.g., objects, faces, body parts, geometric shapes), but have preserved spatial navigation abilities (Farah, 1990). This finding further supports the causal relationship between the ventral pathway and object identification. On the other hand, patients with optic ataxia, who have lesions of the posterior parietal cortex, have difficulty reaching toward visual objects even through they can recognise them (Perenin & Vighetto, 1988). These patients therefore seem capable of identifying what the object is, even if they cannot register where it is in space, providing further evidence for the role of the dorsal pathway in spatial perception. This combination of animal and human neurophysiological evidence provides strong support for Ungerleider and Mishkin's (1982)

hypothesis that the ventral occipitotemporal pathway plays a key role in object perception, but not spatial perception, whereas the dorsal occipitoparietal pathway is specialised for spatial perception, but not object recognition.

Goodale and Milner (1992; see also, Goodale, 2008; Goodale, 2013) make a similar distinction between ventral and dorsal visual processing streams, but argue that the functional role of the dorsal stream is not specific to spatial perception. Instead, they propose the dorsal stream is responsible for processing visual information in the service of goal-directed action (a 'how' stream). For example, while patients with optic ataxia who have dorsal stream lesions show deficits in their ability to reach toward the correct object location, their reaching behaviour is also slow and uncoordinated, and they have difficulty adjusting their hand to suit the appropriate orientation, or the width of their grasp to match an object's size (Perenin & Vighetto, 1988). Similar deficits in visually guided grasping with preserved object recognition abilities have been noted in patients who have recovered from Balint's syndrome – an impairment which also arises from parietal lobe damage (Gross, 1973). These studies therefore suggest that parietal lobe damage does not just lead to deficits in spatial vision, but also in action-related reaching and grasping (Goodale & Milner, 1992). By contrast, patients with visual agnosia who have damage to the ventral stream show the opposite pattern of behaviour: They can display appropriate grasping behaviours, but have trouble identifying the size, shape or orientation of visual targets (Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). Based on this neurophysiological work, Goodale and Milner (1992; see also, Goodale, 2008; Goodale, 2013) propose that visual cortex projections to the parietal lobe are responsible for the processing of action-related information about an object, in addition to its spatial location (as initially suggested by Ungerleider & Mishkin, 1982), whereas projections to the temporal lobe provide information needed for the perceptual experience of an visual object and its attributes.

While these two-system accounts provide broad frameworks for understanding how the brain perceives the features and spatiotemporal properties of an object, and generates an appropriate action plan to interact with it, neither of these neural pathways map directly onto the cognitive mechanisms proposed by Pylyshyn (1989, 1994; 2001) and Kahneman et al. (1992). Put differently, it is unclear how representations generated from individuating an object and identifying its featural attributes are reflected in the brain. To address this question, Xu and Chun (2009) put forward their neural object file theory, which implicates a specific set of occipital and parietal brain regions in object individuation and identification. Specifically, Xu and Chun define object individuation as the ability to select

up to four objects based on their spatial locations, and to create a set of object files representing these stimuli (Kahneman et al., 1992). Individuation involves more than just indexing an object (i.e., beyond the initial assignment of FINSTs; Pylyshyn, 1989), such that the representations generated during this operation are stable perceptual units that can maintain consistency over time and space (Rensink, 2000). Object representations during individuation have a coarse resolution and contain very little, if any, information relating to the featural properties of the associated stimuli. In object identification, on the other hand, attributes from a subset of individuated objects are analysed and integrated (i.e., the contents of the corresponding object files; Kahneman et al., 1992), and there is sufficient information available to recognise an object as familiar or novel. Importantly, the number and precision of object features encoded depends on the complexity of the task demands, such that fewer features can be encoded under higher task demands (Alvarez & Cavanagh, 2004; Xu & Chun, 2006).

The neural object file theory was initially based on the findings of a functional magnetic resonance imaging (fMRI) investigation by Xu and Chun (2006). This study aimed to resolve the debate as to whether visual short-term memory (VSTM) capacity depends on the complexity of the task or stimulus demands (Alvarez & Cavanagh, 2004; Xu, 2002), or instead reflects the number of unified object ‘slots’ that are filled, independent of complexity (Luck & Vogel, 1997; Zhang & Luck, 2008). In this experiment, observers were briefly presented a sample display containing one to four, or six black, elongated shapes that they had to remember over a short delay (see Figure 3). A single test item then appeared. Observers had to either detect whether there had been a simple feature change (detect the presence/absence of a gap in the centre of the test shape) or a complex feature change (detect whether the shape outline changed). Blood oxygen level dependent (BOLD) activity, measured with fMRI, in the superior intra-parietal sulcus (IPS) and lateral occipital complex (LOC) increased with the number of items held in VSTM for simple, but not complex, shape features. Conversely, activity in the inferior IPS tracked the number of objects held in VSTM, regardless of task complexity. In addition, in a follow-up experiment where all objects were presented sequentially at a central location, rather than at peripheral locations, activity increased with set size up to VSTM capacity in the superior IPS and LOC, but not in the inferior IPS (as the spatial locations did not differ across set sizes). These findings were taken as evidence that the inferior IPS reflects an indexing mechanism that is capable of selecting a fixed number of objects based on spatial locations, regardless of their featural properties (object individuation). On the other hand, the superior IPS and LOC are involved in identification and feature extraction, and

consequently are sensitive to a fixed amount of featural information, rather than the physical number of objects present (object identification).

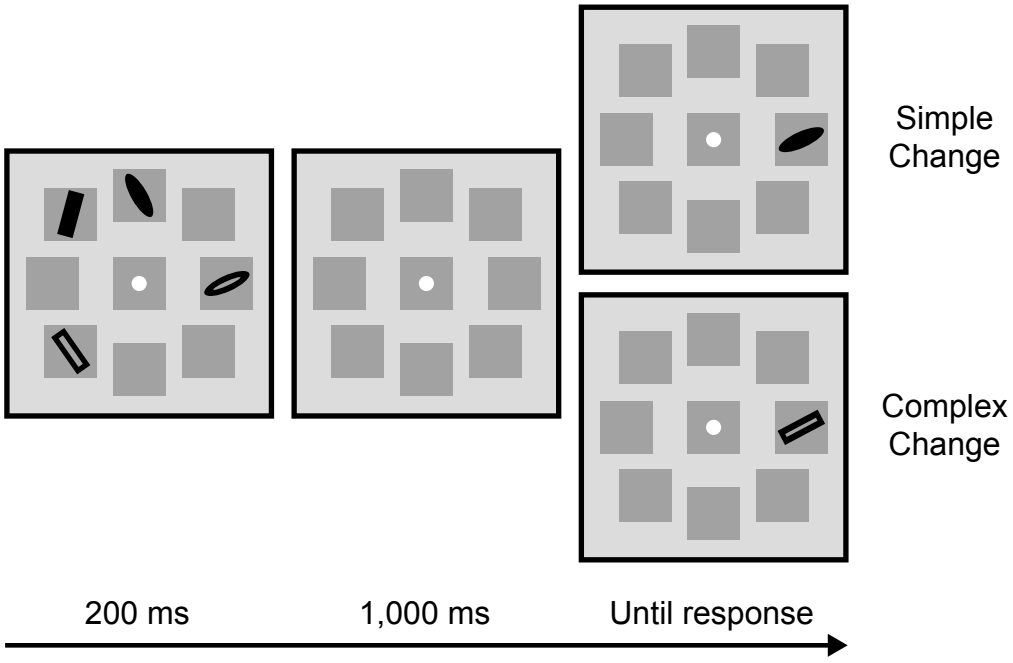

Figure 3. Schematic representation of a visual short-term memory paradigm. Each trial begins with a sample display consisting of one to four or six black shapes. Participants' task is to remember the featural properties of these shapes over a short retention interval. A single test item then appears, and this item either matches one of the previous sample items or not. If there is a featural change at test, it could either be a simple change (i.e., the presence or absence of a gap) or a relatively complex change (i.e., a change in the shape outline). This figure was reproduced from Xu and Chun (2006) with permission from Nature Publishing Group.

A follow-up study by Xu (2009) investigated the apparent dissociation between the neural substrates associated with object individuation (inferior IPS) and identification (superior IPS and LOC) by testing the effect of object repetition. Based on the neural object file theory, Xu predicted that because object individuation relies on information about location but not identity, brain areas involved in individuation should treat four identical objects in the same way as four different objects (as these two conditions have the same number of objects). On the other hand, brain areas that support object identification would respond differently to four identical and four different objects, but should treat four identical objects the same as a single instance of the same object (as

these two conditions contain the same amount of identity information). Xu (2009) used a similar VSTM paradigm to Xu and Chun (2006; see Figure 3), except now the sample display could consist of one shape, four identical shapes or four different shapes. BOLD activity in the inferior IPS was reduced for one-object displays relative to both of the four-object displays, which did not differ from each other. However, the superior IPS and LOC showed a greater response for four-different-object displays compared with both the four-identical-object and one-object displays. Thus, consistent with the predictions of the neural object file theory, Xu (2009) found that the inferior IPS tracked the spatial locations of objects (individuation), whereas the superior IPS and LOC were sensitive to the number of object features (identification). Interestingly, these findings contradict the traditional distinction between 'what' and 'where' visual pathways in the brain (Ungerleider & Mishkin, 1982), and instead suggest that these two types of object information are represented within the parietal cortex (Xu, 2009).

Neural Bases of Individuation Across Time

The research discussed thus far illustrates important aspects of the processes associated with multiple object encoding, but there are still key questions that remain unanswered. In particular, we currently do not have a clear understanding of the systems-level neural substrates associated with representing stimuli as distinct perceptual events (i.e., the process of individuation). An important issue concerns how objects are individuated across time (*temporal individuation*). The paradigms that have typically been used to investigate object individuation manipulate either the number of spatial locations that contain an object (e.g., VSTM paradigms by Xu and colleagues; object reviewing paradigms by Kahneman and colleagues), or vary spatial and temporal properties concurrently (e.g., multiple object tracking tasks by Pylyshyn and Storm). As a result, it is currently unknown how *purely* temporal information contributes to object individuation, and particularly, how this process is represented in the brain. The single neural substrate implicated in object individuation (inferior IPS) has only been studied in a spatial episodic context (Xu, 2009), meaning that we do not know whether this region – or indeed other brain areas – are also involved when an observer must only rely on temporal cues to register distinct stimuli.

Repetition blindness (RB) is a behavioural phenomenon that could be employed to address this issue, as it is thought to provide an index of the temporal capacity limits of object individuation (Kanwisher & Potter, 1989; Mozer, 1989; Park & Kanwisher, 1994). In Kanwisher's pioneering experiments, observers were presented with a rapid serial visual

presentation (RSVP) stream of words that formed a sentence, one at a time, and their task was to report the full sentence at the end of the stream. There were two key manipulations: The identity of the two critical items in the stream and the number of distractor words (lags) between the two critical items. Specifically, the critical items could either share the same identity (repeated items) or have different identities (non-repeated items). Temporal lag was varied such that the two critical items appeared relatively close in time (e.g., 200 ms) or further apart (e.g., 600 ms). The classic RB finding was that when the two critical items appeared in close temporal proximity, observers were poorer at reporting the second item if it had the same (versus a different) identity to the first critical item. RB has now been demonstrated for a wide range of stimuli including alphanumeric items (Chun, 1997), colours (Kanwisher, 1991) and objects (Harris & Dux, 2005a, 2005b), and can even occur for words that are non-identical, yet orthographically similar (e.g., "reach" and "react"; Bavelier, 1994). Moreover, equivalent performance decrements for repeated targets are seen when participants are asked to detect, rather than identify, the target items (e.g., Coltheart & Langdon, 2003; Johnston, Hochhaus, & Ruthruff, 2002; Kanwisher, 1987), suggesting that RB reflects, at least to some extent, a perceptual processing limitation.

A prominent theoretical account proposed by Kanwisher (1987; also see, Chun, 1997; Wyble, Bowman, & Nieuwenstein, 2009) suggests that RB reflects a failure of type-token binding, and draws on a similar distinction to that proposed by Kahneman and Treisman (1984). Kanwisher predicts that as each item appears in the RSVP stream, its type is activated and a token is created to register it as a distinct episodic event. These two representations are linked together through the process of *token individuation*, in which the activated type is bound to the corresponding token. Once a type has been bound to a specific token, there is a refractory period during which that same type cannot be linked with another token. It is this inhibition of the second repeated item's token individuation that gives rise to RB. That is, the observer can successfully individuate the first occurrence of the repeated item, but due to the refractory period, they cannot link the token for the second occurrence with its type and thus, they only perceive a single item. Importantly, activation of the type representation for the second repeated item is unaffected, as shown by enhanced performance on repeated trials (repetition *priming*) when observers are only required to report the second target (Kanwisher & Potter, 1990; Shapiro, Driver, Ward, & Sorensen, 1997; but also see, Luo & Caramazza, 1995). Further, RB is reduced under conditions that enhance the episodic distinctiveness between two targets – such as presenting targets in a different colour to distractors (Chun, 1997; Dux &

Coltheart, 2008) or cueing attention to targets with an irrelevant sound (Chen & Yeh, 2008) – which make it easier to mark each occurrence.

Although Kanwisher's account argues for a perceptual locus for RB, other models propose that this deficit arises at a later stage of information processing. These accounts instead argue that RB reflects a memory retrieval bias or failure. This suggestion is based on findings that observers can be blind to the second *retrieved* repeated item, rather than the second *seen* repeated item (Fagot & Pashler, 1995), and that this deficit does not occur if the second critical item is cued at the end of the stream (Armstrong & Mewhort, 1995). It is difficult to interpret these results, however, as the paradigms used in these experiments differ from standard RB tasks (Neill, Neely, Hutchison, Kahan, & VerWys, 2002), and they typically result in performance that is close to floor (Johnston et al., 2002). In addition, direct evidence against such memory retrieval accounts comes from paradigms that have low memory demands or require online responses, but still yield RB (Anderson & Neill, 2002; Dux & Marois, 2007; Johnston et al., 2002).

RB has been studied almost exclusively using behavioural methods (but also see, for electrophysiological studies, Koivisto & Revonsuo, 2008; Schendan, Kanwisher, & Kutas, 1997). Consequently, the neural substrates of this deficit and related individuation processes are currently unknown. However, there has been extensive research into related RSVP phenomena, such as the attentional blink. Like RB, the attentional blink reflects a failure of perceptual awareness associated with identifying the second of two targets when they appear in close together in an RSVP stream (e.g., 200-500 ms; Chun & Potter, 1995; Raymond, Shapiro, & Arnell, 1992). The attentional blink, however, occurs when the two targets have different identities and therefore reflects the temporal capacity limits of object identification (Chun, 1997). Importantly, Chun (1997) demonstrated a double dissociation between RB and the attentional blink, where the former, but not the latter, deficit was reduced when targets were presented in different colours (which enhanced their episodic distinctiveness); the converse was true when targets and distractors were highly discriminable (which enhanced target identification).

A common approach to studying RSVP deficits in the brain is to contrast BOLD activity between trials where the observer correctly reports the second target (hits) with trials in which they fail to report the second target (misses). Using this comparison, neuroimaging studies have localised the attentional blink bottleneck to regions of the lateral frontal cortex and posterior parietal cortex (Marois, Yi, & Chun, 2004), with several other studies also implicating ventral occipitotemporal areas (Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marcantoni, Lepage, Beaudoin, Bourgouin, &

Richer, 2003). The discrepant results concerning the role of occipitotemporal areas in the attentional blink appear to be driven by subtle paradigm differences, implicating the role of task difficulty in how this deficit is reflected in brain activity (Johnston, Shapiro, Vogels, & Roberts, 2007; Shapiro, Johnston, Vogels, Zaman, & Roberts, 2007). In Chapter 2, I present an fMRI study that employed an RB approach to explore the brain regions that are recruited during individuation of stimuli across time and those that are active when temporal individuation fails (i.e., the neural locus of RB).

Relationship Between Object Individuation and Identification

A second outstanding question concerns the nature of object individuation and identification in the brain: Are these two processes dissociable or do they share common neural substrates? A key tenet of the neural object file theory is that object individuation and identification are supported by distinct brain areas (Xu & Chun, 2009), whereby individuation is underpinned by the inferior IPS and identification is subserved by the superior IPS and LOC. As Xu and Chun only analysed activity in these three occipitoparietal areas, we do not know the extent to which object individuation and identification might be represented in other brain regions. It is possible that these processes manifest in a broader set of brain regions and that there is overlap between the two beyond the focal neural substrates implicated in the neural object file theory.

The neural object file theory is based on studies that used memory tasks to investigate individuation and identification processes. The RB paradigm used to explore the temporal individuation in Chapter 2, however, likely tapped this process at an earlier perceptual stage of processing. In order to test the specific neural dissociation proposed by Xu and Chun (2009), I adopted a similar approach and looked at the relationship between object individuation and identification during encoding, storage and retrieval stages of VSTM. Of interest, Baars and Franklin (2003) have argued that the contents of working memory represent the information that reaches awareness and is available for conscious report. Given the suggested links between memory processes and consciousness (e.g., Andrade, 2001; Baddeley, 1992), current models of consciousness might provide alternative insights into how individuation and identification processes might be reflected in the brain.

The global workspace model is a dominant theory of consciousness. It suggests that processes that contribute to visual awareness – including potentially individuation and identification – operate across a widespread neural network. Specifically, this model predicts that the human brain contains two computational spaces that give rise to

perceptual awareness (Baars & Franklin, 2003; Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001). The first is a set of specialised modules dedicated to processing information for a given mental or sensory operation. These specialised hubs cannot communicate with each other directly, but instead do so via a second computational space. This *global workspace* consists of a set of neurons that are distributed across the brain, and this workspace facilitates the exchange of information between specialised modules via long-range reciprocal connections. Top-down attentional mechanisms control which modules provide input to the global workspace, and thus reach consciousness. The workspace is therefore not fixed to a specific set of brain areas, but dynamically changes as workspace neurons in different brain circuits are temporarily activated, and deactivated, at distinct points in time. Because object individuation and identification are both crucial for encoding visual objects for conscious report, it is possible that they may operate across a distributed neural network. In Chapter 3, I present an fMRI study that aimed to test the apparent dissociation between object individuation and identification proposed by Xu and Chun (Xu, 2009; Xu & Chun, 2009), with a particular focus on analysing activity across a large set of frontal, parietal and occipital regions.

Multi-Voxel Pattern Analysis

The questions introduced above are directed toward understanding the neural substrates of object individuation. There are several approaches that can be employed when analysing fMRI data in order to map a particular cognitive function to a specific brain region. Neuroimaging studies on object individuation and identification to date have relied solely on conventional univariate analyses (e.g., Xu, 2007; Xu, 2008, 2009; Xu & Chun, 2006). Such univariate approaches contrast BOLD activity between separate conditions to identify individual voxels in which the BOLD signal is greater under one condition than another. To increase the sensitivity of this analysis, activity is averaged across all significant voxels in a given region to determine whether there is an overall amplitude difference between conditions. A consequence of this type of approach is that it ignores the contribution of other non-significant voxels that might still contain information about the different conditions, yet do not show a great enough amplitude difference to reach significance (Norman, Polyn, Detre, & Haxby, 2006).

An alternative approach is multi-voxel pattern analysis (MVPA; also referred to as decoding; for reviews, see Norman et al., 2006; Tong & Pratte, 2012). Unlike conventional approaches, MVPA assesses whether the pattern of activity recorded across a group of voxels, in a given region of interest, differs systematically between conditions. As this

analysis is only concerned with absolute, rather than relative, changes in activity between conditions, it has the potential to distinguish between conditions that do not differ in overall BOLD amplitude. MVPA relies on a classifier algorithm that is trained to discriminate between the activity patterns across a group of voxels, where it attempts to develop a decision boundary that best separates the voxel responses corresponding to each condition. The classifier is then tested on its ability to distinguish between novel activity patterns associated with each condition. If the classifier can reliably discriminate between the patterns of activity observed across the conditions at test, one can infer that the voxels corresponding to that brain region code for the information contained in those conditions.

In one of the first uses of this technique, Kamitani and Tong (2005; see also, Haynes & Rees, 2005) analysed activity in early visual areas in response to grating stimuli presented at different orientations. Orientation-selective cortical columns were first described in primary visual cortex in monkeys and cats using single-unit electrophysiology measures (e.g., Blasdel, 1992; Hubel & Wiesel, 1962), but it had been found that these columns were to fine grained to be detected using the typical resolution of human fMRI and univariate analysis methods (Kim, Duong, & Kim, 2000). Kamitani and Tong hypothesised that each individual fMRI voxel should nevertheless show a weak, but true, bias toward its preferred orientation. Specifically, they reasoned that if they pooled activity across a group of weakly tuned voxels, they might be able to detect a systematic change in activity with orientation in the human visual system. Consistent with this prediction, Kamitani and Tong found that the ensemble patterns of activity in early visual cortex could discriminate between different visual orientations. When voxel activity was analysed using the conventional univariate approach, however, no difference was found in the overall amplitude to each orientation. This study demonstrates how MVPA can be very sensitive to small but reliable changes in BOLD activity that may be missed in univariate analyses.

The advantage of MVPA over conventional univariate analyses has also been demonstrated beyond the perception of basic visual features. Vickery, Chun and Lee (2011) used MVPA to explore the extent to which reward signals are represented throughout the brain. Traditionally, reward-related processes had been associated with discrete parts of the ventral striatum, medial prefrontal cortex, orbitofrontal cortex, posterior cingulate and inferior parietal cortex (Elliott, Friston, & Dolan, 2000; Kable & Glimcher, 2007; Kahnt, Heinzle, Park, & Haynes, 2010; Knutson, Fong, Bennett, Adams, & Hommer, 2003; Rushworth & Behrens, 2008; Vickery & Jiang, 2009). Vickery et al. had participants play a matching-pennies game against a computer opponent. MVPA revealed that wins (trials in which the participant’s choice matched the computer’s choice) could be

reliably discriminated from losses (trials where the participant's choice did not match the computer's choice) in a large number of cortical regions (37 out of 43 regions of interest). This coverage greatly exceeded that shown in the univariate analysis (7-9 regions). These findings demonstrate how MVPA is more sensitive at detecting distributed signals associated with higher-level cognitive processes, compared with univariate analyses. Because the present work into object individuation and identification has relied solely on univariate techniques, it is possible that these findings might underestimate the extent to which these processes are reflected in brain activity. In the fMRI studies reported in Chapters 2, 3 and 4, I analysed BOLD activity using MVPA (as well as conventional univariate analyses in Chapters 2 and 3) to better characterise the extent to which individuation and identification processes are represented in the brain.

Despite its obvious advantages, MVPA also has some important limitations. As MVPA only looks for a difference in BOLD activity, rather than the direction of the effect (as in univariate analyses), confounds that would usually have been ruled out due to averaging procedures can sometimes remain (Todd, Nystrom, & Cohen, 2013). Reaction time is often pointed out as a possible alternative source of differences in activity patterns, and is taken as a proxy for general task factors such as difficulty, mental effort and time on task. In an empirical demonstration of this potential problem, Todd et al. (2013) used data from an fMRI study by Woolgar, Thompson, Bor, and Duncan (2011) that looked at how task rules are represented in the brain. Todd et al. found that when reaction time was regressed out, there were no longer any differences in the patterns of activity corresponding to the task rules. This finding suggests that the observed differences in the MVPA results were driven by reaction time, rather than the manipulated task rules (for a counter commentary, see, Woolgar, Golland, & Bode, 2014). Reaction time is not always an ideal measure of general task effects, however, as removing reaction time differences would also remove some of the variability evoked by the conditions themselves. Nonetheless, one can alleviate doubts about the influence of factors like reaction time in MVPA by comparing two conditions that produce similar reaction times but still differ on the critical variable of interest.

Timecourse of Object Individuation

The final outstanding question of this thesis concerns the stage of information processing at which object individuation occurs. Due to the sluggish nature of the BOLD signal, standard event-related and blocked fMRI designs lack the temporal resolution to delineate the timecourse of cognitive processes (an exception is time-resolved fMRI

designs; Dux, Ivanoff, Asplund, & Marois, 2006). Electroencephalography (EEG), on the other hand, can detect rapid changes in neural activity within the time range of milliseconds, making it an ideal technique for investigating how object individuation and identification processes manifest in the brain over time. For example, Vogel, Luck, and Shapiro (1998) used EEG to isolate the temporal locus of the attentional blink. These authors found that the amplitude of the P3 component in response to the second target was reduced during the blink time window, suggesting that this deficit occurs before (or perhaps at the same time that) the representation is encoded into working memory (Donchin & Coles, 1988).

There has been a wealth of studies conducted into the encoding and storage of object identities into working memory using VSTM tasks and EEG (e.g., Gao et al., 2011; Ikkai, McCollough, & Vogel, 2010; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). For example, Vogel and Machizawa (2004) briefly presented sample displays that contained one to ten coloured squares in each hemifield, and observers were asked to remember the colours in one of the hemifields. After a short delay, a test display containing the same number of items appeared. Participants had to indicate whether the sample and test displays were identical or different. Behaviourally, participants could perform this task well for arrays containing four or fewer items, at which point performance declined dramatically with further set size increases (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001). These authors analysed the contralateralised delay activity (CDA; also known as sustained posterior contralateral negativity) in response to each set size by subtracting activity recorded over posterior occipitoparietal electrodes ipsilateral to the attended hemifield from activity at the corresponding contralateral electrodes. This event-related potential (ERP) component is characterised by a negative-going waveform that begins approximately 200-300 ms after stimulus onset (Woodman & Luck, 1999). Vogel and Machizawa (2004) found CDA amplitude increased with set sizes up to four items and then plateaued for larger set sizes. These findings suggest that the CDA component reflects the number of identities that can be successfully encoded into working memory.

To directly test whether the CDA component reflects the amount of identity information present in the display, rather than the number of spatial locations, Gao et al. (2011) adopted a similar approach to Xu (2009). The idea here was that if the CDA specifically tracks identity information, there should be a difference in amplitude between four-identical-object and four-different-object displays (which only differ in the number of object identities), but no difference between one-object and four-identical-object displays

(since identity information is held constant across these two display types). Consistent with this prediction, Gao et al. found CDA amplitude was reduced for four-different-object displays, relative to both four-identical-object and one-object displays, which did not differ from each other. The source of this amplitude difference was further localised to the superior IPS, which is line with this region's claimed role in object identification in short-term memory (Xu, 2007, 2009; Xu & Chun, 2009). These results are supported by converging evidence showing that CDA amplitude is equivalent for objects when they are presented simultaneously at different locations or sequentially at a central location (Ikkai et al., 2010). Together, these studies suggest that the CDA component tracks the number of identities held in working memory, independent of the number of distinct spatial locations at which they appear.

Similar efforts have been made to isolate the temporal locus of object individuation using a range of experimental paradigms that likely tap different perceptual processing stages. The results of ERP studies on RB are not as clear, but suggest that correctly identified, repeated targets, compared with missed repetitions, evoke greater positivity over posterior temporal electrodes between 150 and 400 ms after stimulus onset (Koivisto & Revonsuo, 2008; Schendan et al., 1997). Other studies have used paradigms such as multiple object tracking (Drew & Vogel, 2008), enumeration (Ester, Drew, Vogel, & Awh, 2012; Pagano & Mazza, 2012), visual search (Anderson, Vogel, & Awh, 2013a) and change detection (Anderson, Vogel, & Awh, 2011; Anderson, Vogel, & Awh, 2013b), and found the number of objects to be individuated modulates the amplitude of a negative-going potential referred to as the N2pc component (Anderson, Vogel, & Awh, 2014). Like the CDA, the N2pc reflects a difference waveform between activity measured over posterior electrode sites contralateral, compared with ipsilateral, to the attended stimulus, that peaks around 200-300 ms after stimulus onset (Luck & Hillyard, 1994). This N2pc component has also been associated with the selection of targets among distractors in visual search (Jolicœur, Brisson, & Robitaille, 2008; Luck & Hillyard, 1994) and the involuntary capture of attention by salient distractors (Hickey, McDonald, & Theeuwes, 2006).

In one of these studies, Ester et al. (2012) used the N2pc to investigate enumeration – one's ability to rapidly determine the numerosity of a group of visual stimuli without the need to count them individually (Kaufman, Lord, Reese, & Volkmann, 1949) – as an index of object individuation. Typically, observers are able to accurately report the number of items that appear in set sizes up to approximately four items (a process referred to as *subitizing*), and errors increase dramatically for larger set sizes (Piazza, Fumarola,

Chinello, & Melcher, 2011; Revkin, Piazza, Izard, Cohen, & Dehaene, 2008; Trick & Pylyshyn, 1993; Trick & Pylyshyn, 1994). These behavioural studies suggest that subitizing is underpinned by one's ability to simultaneously individuate items in a display, and that it is constrained by a capacity limit. Ester et al. (2012) presented observers with a spatial cue, followed by a set of black squares in both hemifields where a subset of items was presented in the target/non-target colour (blue and green, or vice versa). There were one to twelve target items on each trial, with the same number of non-target items in the unattended hemifield. Critically, N2pc amplitude increased linearly with target set size up until about three items, at which point it plateaued (the same point at which behavioural performance starts to deteriorate). These findings provide direct evidence that the N2pc component reflects the ability to individuate small sets of target items and is fixed to the capacity limit of this process.

What is less clear is whether there is also evidence of object individuation at time points prior to the onset of the N2pc component. There is some evidence that a negative component that peaks around ~120-180 ms (N1) is modulated by the number of targets when they appear alone, but not when they appear with distractors (i.e., which equates the total number of items across set sizes; Mazza, Pagano, & Caramazza, 2013). This finding suggests that this component might instead reflect the amount of visual information presented, rather than the process of individuation (also see, Hyde & Spelke, 2009, 2012). The paradigms used in these prior ERP studies are potentially problematic as they confound manipulations of object individuation (e.g., the number of distinct coloured targets among distractors), with low-level visual differences (e.g., hue, luminosity, eccentricity). In Chapter 4 of this thesis, I report an EEG/fMRI project employing a novel enumeration paradigm that removed these low-level visual confounds. I explored the timecourse of object individuation to determine whether there is evidence of this process at early perceptual stages of processing, and in the BOLD response of early sensory brain regions. In addition, I assessed how selective spatial attention modulates the timecourse of individuation by examining individuation processes for target and distractor stimuli.

Summary

Object individuation is vital for the accurate perception of an object as a distinct entity and for encoding it into a durable form that can be maintained over spatiotemporal changes. Despite the theoretical and empirical interest in this process over several decades, it is still not clear how object individuation occurs in the human brain, how it relates to other processes like identification, or what the temporal dynamics of this process

are. These are the questions I address in this thesis. In Chapter 2, I demonstrate the role of a distributed set of occipital, frontal and parietal brain regions in temporal individuation during perception. Not only does this study provide the first evidence for the neural substrates that support the temporal aspects of early object individuation, but the widespread neural involvement also dramatically contrasts with the single neural correlate of individuation that is currently proposed by the neural object file theory (Xu & Chun, 2009). This study also isolates the individuation bottleneck that underpins RB to a higher-level premotor area.

Given the widespread nature of temporal individuation in the brain, the fMRI study reported in Chapter 3 aimed to test the proposed neural dissociation between object individuation and identification in VSTM (Xu & Chun, 2009) using distributed regions of interest and a more sensitive MVPA approach. Contrary to what is proposed in the neural object file theory, I found object individuation and identification are underpinned by distributed and overlapping neural substrates, and the specific brain regions that support each process vary across distinct processing stages in VSTM. In the final study of this thesis (Chapter 4), I used EEG to explore the temporal dynamics of object individuation and the extent to which this is influenced by selective attention. I found evidence of object individuation at an early perceptual ERP component (100-140 ms after stimulus onset) – a time window that precedes the N2pc, which has previously been associated with this operation. Moreover, I observed distinct timecourses for targets and distractors, suggesting a key role of attention in the registration of stimuli. In a subsequent fMRI experiment, I also demonstrated that individuation draws on early visual sensory areas, which are potential sources of this ERP effect. Together, this package of work advances our understanding of how object individuation is implemented in the human brain.

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CHAPTER 2: THE NEURAL BASIS OF TEMPORAL INDIVIDUATION AND ITS CAPACITY LIMITS IN THE HUMAN BRAIN

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Abstract

Individuation refers to individuals' use of spatial and temporal properties to register an object as a distinct perceptual event relative to other stimuli. Although behavioural studies have examined both spatial and temporal individuation, neuroimaging investigations of individuation have been restricted to the spatial domain, and at relatively late stages of information processing. Here we used univariate and multi-voxel pattern analyses of functional magnetic resonance imaging data to identify brain regions involved in individuating temporally distinct visual items, and the neural consequences that arise when this process reaches its capacity limit (Repetition Blindness [RB]). First, we found that regional patterns of blood oxygen level dependent activity in a large group brain regions, which are involved in 'lower-level' perceptual and 'higher-level' attentional/executive processing, discriminated between instances where repeated and non-repeated stimuli were successfully individuated – conditions that placed differential demands on temporal individuation. These results could not be attributed to repetition suppression, stimulus or response factors, task difficulty, regional activation differences, other capacity-limited processes or artifacts in the data or analyses. Consistent with the global workplace model of consciousness, this finding suggests that temporal individuation is supported by a distributed set of brain regions, rather than a single neural correlate. Second, conditions that reflect the capacity limit of individuation – instances of RB – modulated the amplitude, rather than spatial pattern, of activity in the left hemisphere premotor cortex. This finding could not be attributed to response conflict/ambiguity and likely reflects a candidate brain region underlying the capacity-limited process that gives rise to RB.

Behaviour is shaped by how individuals perceive their external environment. As our environment provides far too much sensory information for all of it to be processed up to awareness, we rely on selective attention mechanisms to reduce the overwhelming amount of available information to a manageable set of relevant items and/or sources (Pashler, 1998). Merely attending to sensory information, however, does not guarantee that it will reach awareness or impact behaviour; such information needs to be encoded in relation to the observer's pre-existing rules, goals and knowledge (Cohen, Cavanagh, Chun, & Nakayama, 2012).

In vision, a key operation implicated in successful object encoding is *individuation*, the process by which observers use spatial and temporal episodic cues to determine where and when an object appeared (e.g., Chun, 1997; Kahneman, Treisman, & Gibbs, 1992; Mitroff, Scholl, & Noles, 2007; Pylyshyn, 1989, 1994; Xu & Chun, 2009). This process is crucial for registering individual items as distinct perceptual events and is thought to underlie observers' impaired ability at discriminating between separate occurrences of objects with the same identity, relative to those with different identities (Kanwisher, 1987). Although observers show capacity limits associated with individuating items across both time and space (e.g., Kanwisher, 1991; Kanwisher & Potter, 1989; Luo & Caramazza, 1995, 1996), and previous studies have begun to identify the neural correlates of spatial individuation (e.g., Jeong & Xu, 2013; Xu, 2009; Xu & Chun, 2006; Xu & Chun, 2007), no study has identified the neural substrates underlying temporal individuation. Here we used functional magnetic resonance imaging (fMRI) to investigate the brain regions and mechanisms that are involved in the successful individuation of temporally distinct objects during encoding, and how disruptions to this process are represented in the brain.

Initial fMRI investigations into individuation have identified a candidate brain area that might store individuated object representations in visual short-term memory (Jeong & Xu, 2013; Xu, 2009; Xu & Chun, 2006, 2007). Specifically, Xu (2009) found that activity in the inferior intra-parietal sulcus (IPS) was sensitive to the number of previously individuated items, regardless of the overall number of perceptual features. This finding suggested that the inferior IPS is involved in storing spatially individuated items, and activity in this region could be dissociated from other regions involved in storing object identities. Based on their findings, Xu and Chun (2009) proposed the neural object file account, which argues that object individuation is supported by the inferior IPS.

Although Xu and colleagues' investigations suggest a neural basis for spatial individuation, their work focused on a few posterior brain regions and did not explore the

contributions of other ‘higher-level’ brain areas. As recent models of consciousness propose that awareness involves a distributed set of psychological processes and neural substrates (Baars & Franklin, 2003; Dehaene, Sergent, & Changeux, 2003; Sergent & Dehaene, 2004), individuation could be underpinned by a more diffuse group of regions. In addition, the inferior IPS appears to store individuated representations, yet storage reflects the consequences of individuation rather than the generation of such representations. We are interested in the brain regions that are involved in actively individuating an object during encoding. To address this issue, we directly compared (1) conditions that place high or low demands on temporal individuation processes during encoding, and (2) conditions of successful versus unsuccessful registration of identical stimuli. To explore the possible role of a more diverse set of regions, our analyses compared changes in blood oxygen level dependent (BOLD) activity across a wide set of cortical areas.

We employed the Repetition Blindness (RB) phenomenon to investigate temporal individuation. RB refers to the finding that observers are poorer at reporting two targets embedded in a rapid serial visual presentation (RSVP) if they have the same identity, relative to different identities (Kanwisher, 1987; Park & Kanwisher, 1994). Kanwisher’s (1987) prominent account of RB argues that token information (spatio-temporal properties of an object) for the second target cannot be bound to its type representation (featural and conceptual properties of an object) when it activates the same type as the first target within a short space of time. RB does not reflect a failure to create a type or token for a repeated item, but rather reflects a limitation associated with binding these two representations for conscious report. This deficit is thought to reflect a capacity limit of individuation because it is strongest when the two targets appear within close temporal or spatial proximity (e.g., Chun, 1997; Kanwisher, 1987). Kanwisher’s account views RB as a perceptual phenomenon, yet other models propose that RB has a later locus, reflecting a retrieval bias or failure (Fagot & Pashler, 1995; Whittlesea & Masson, 2005). However, because RB has been observed in tasks that have very low memory demands or require immediate responses, there appears to be a strong perceptual component to the effect (e.g., Anderson & Neill, 2002; Dux & Marois, 2007; Johnston, Hochhaus, & Ruthruff, 2002).

We therefore used a RB paradigm to vary the trial-level demands of successfully individuating two sequentially presented stimuli as distinct items by manipulating whether the critical items had the same or different identities. This approach allowed us to investigate two novel questions: First, can temporal individuation be localized to a single brain region (see, Jeong & Xu, 2013; Xu, 2009; Xu & Chun, 2006, 2007), or does this process arise from widespread encoding throughout the brain as suggested by recent

models of consciousness (Baars & Franklin, 2003; Dehaene et al., 2003; Sergent & Dehaene, 2004)? We expected that activity in brain regions involved in temporal individuation would be modulated by the demands placed on this process, whereby it is more demanding to successfully individuate repeated stimuli than non-repeated stimuli. Second, what neural consequences arise when demands exceed the capacity limit of the individuation process, as reflected by the behavioural RB deficit? We predicted the brain areas that underpin capacity limits that lead to RB would respond differently under conditions where two repeated stimuli were successfully detected compared to when they were not.

Materials and Methods

Participants

We recruited 16 volunteers for two behavioural experiments (*N* = 6 and 10, respectively; 2 males in each) and 28 volunteers for an fMRI experiment (12 males). The mean ages for participants in the three experiments were 26.0 (*SD* = 5.2), 18.8 (*SD* = 1.0) and 23.8 (*SD* = 3.7) years, respectively. Participants were compensated for their time with course credit or payment. Data from five participants were excluded from the fMRI experiment due to excessive head motion (motion greater than 4 mm/degrees in any translational direction or rotation, respectively; henceforth *N* = 23). All participants had normal or corrected-to-normal vision. Four participants from the first behavioural experiment also participated in the fMRI experiment. The University of Queensland Ethics Committee approved the protocol for all the experiments.

Stimuli

The stimulus set used in all the experiments consisted of 56 indoor and 56 outdoor scenes and scrambled versions of each scene (Marois, Yi, & Chun, 2004). All stimuli were presented in grey-scale and subtended 11.8° x 11.8° of visual angle at the viewing distance of 57 cm outside the scanner (scene stimuli measured 6.5° x 6.5° of visual angle inside the scanner, viewed from a distance of 90 cm). In the fMRI experiment, we also used 18 photographs of faces from the NimStim face database (Tottenham et al., 2009) for the localiser task. Face stimuli were presented in grey-scale and subtended 5.2° x 6.5° of visual angle inside the scanner. Experiments were programmed in MATLAB with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Behavioural Experiments

Long inter-trial interval (ITI) RB experiment. We first developed an RB paradigm optimised for fMRI (see Figure 1). This paradigm was based on similar studies that have used pictures or novel objects as stimuli (e.g., Coltheart, Mondy, & Coltheart, 2005; Harris & Dux, 2005a, 2005b). The purpose of the first behavioural experiment was to assess whether our protocol could elicit the standard RB behavioural effect. Each trial began with a fixation cross for 500 ms, followed by an RSVP stream consisting of a forward scrambled scene mask, three sequentially presented intact scenes (first critical scene [C1], distractor scene, second critical scene [C2]) and a backward scrambled scene mask (100 ms/item). We manipulated 'Scene Repetition' within participants, such that both critical scenes either had the same identity (repeat) or different identities (non-repeat). Participants were informed that the distractor scene would never be the same as C1 or C2.

At the end of the RSVP stream, a blank response screen was presented for 3 s, followed by an 8 s ITI (i.e., a slow event-related fMRI protocol). Participants' task was to report one of three response options during the post-trial 3 s window: They could report that a scene was repeated, no scene was repeated or only two scenes were presented (catch trial response, see below). Only response accuracy was emphasised. We also ran a behavioural experiment using this RB paradigm without the long ITI (the next trial began immediately after participants made an untimed response), and the pattern of results were comparable to the present experiment (reported below). We chose to use a paradigm in which participants had to detect the presence of a repetition, rather than identify the critical items, as this was more appropriate for studying RB in the scanner with scene stimuli (i.e., responses were forced-choice and could be made using a button-box). It should be noted that both detection and identification approaches have been used to study RB previously (e.g., Hochhaus & Johnston, 1996; Kanwisher, Kim, & Wickens, 1996; Park & Kanwisher, 1994) and are considered to tap the same individuation processes.

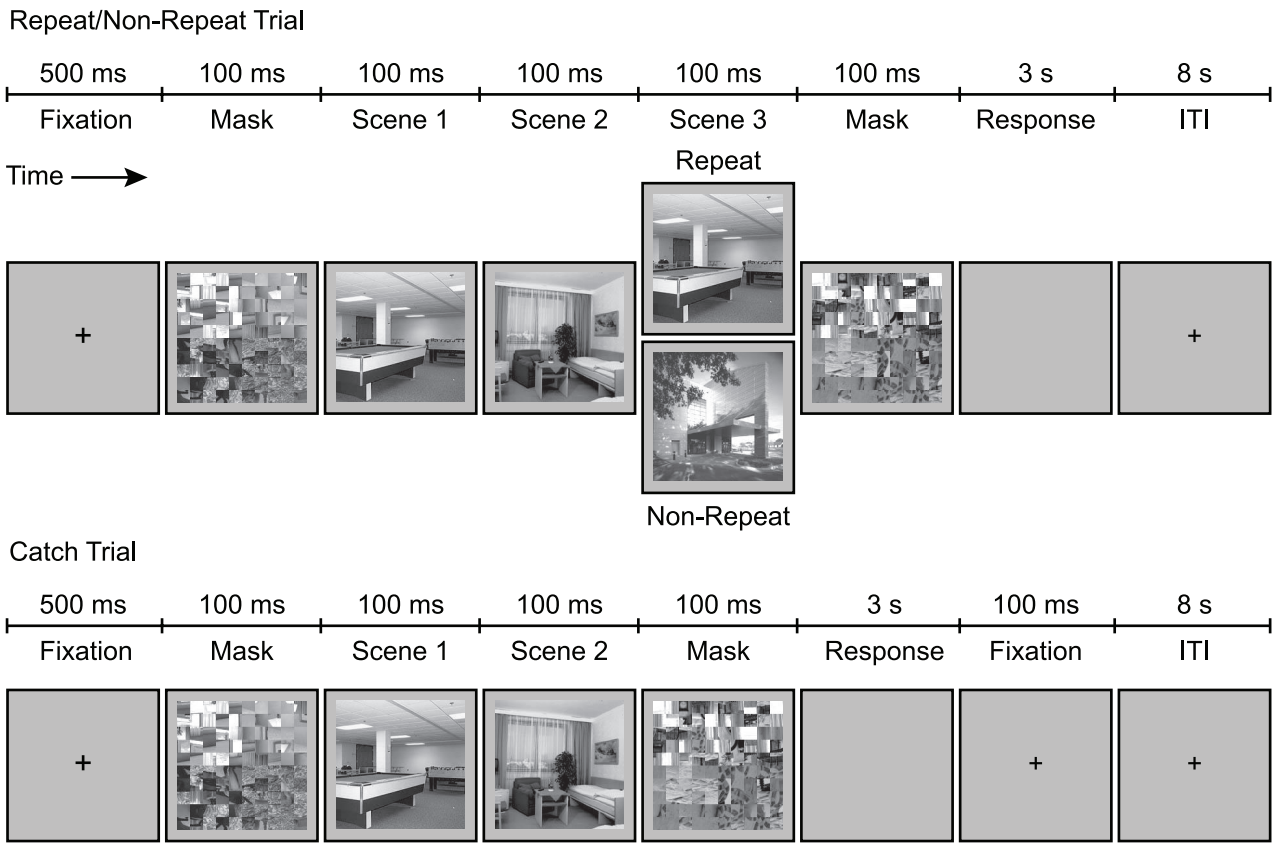

Figure 1. Schematic representation of the repetition blindness paradigm.
On repeat/non-repeat trials, participants were presented with a rapid serial visual presentation (RSVP) stream consisting of a forward scrambled scene mask, three intact scenes (first critical scene, distractor scene, second critical scene), and a backward scrambled scene mask. The two critical scenes were either identical (repeat trial) or different (non-repeat trial). Only two different intact scenes were presented in the RSVP stream on catch trials. Participants reported whether they saw a scene repeated, no scene repeated or only two scenes during the response window. Stimuli are reproduced from Marois et al. (2004) with permission from Elsevier Limited.

As is standard in behavioural investigations of RB, catch trials were included on 20% of trials to reduce the likelihood of participants guessing 'repeat' on trials where they missed the second repeated scene (Dux & Coltheart, 2008; Harris & Dux, 2005a, 2005b). These trials only contained two different intact scenes in the RSVP stream. To ensure catch trials lasted for the same duration as repeat and non-repeat trials (12 s), we included an additional fixation screen for 100 ms between the response window and ITI (see Figure 1).

Participants were provided with an instruction sheet outlining the task and response keys and completed 20 practice trials before testing. There were 6 blocks of 25 test trials

with an equal number of repeat and non-repeat trials. The order of the trial types was random. Behavioural experiments were completed on a 20-inch Dell Trinitron CRT monitor with a refresh rate of 100 Hz using a Mac mini computer.

Lag RB experiment. We conducted a second behavioural experiment to ensure that our RB paradigm specifically tapped the temporal capacity limits of individuation. The attentional blink (AB) is a similar deficit to RB as it too occurs under dual-target RSVP conditions, is characterised by poorer identification of a second target at short inter-target intervals (e.g., 200-500 ms), and is thought to reflect a failure of perceptual awareness (Chun & Potter, 1995; Raymond, Shapiro, & Arnell, 1992). The AB, however, occurs under conditions where the two targets have different identities. Thus, in contrast to RB, the AB reflects the temporal capacity limits of object identification, rather than individuation (Chun, 1997; see also, Dux & Marois, 2009). In an additional behavioural experiment, we confirmed that the observed differences in detection accuracy on repeat and non-repeat trials in the Long ITI RB experiment reflected the temporal capacity limits of individuation, rather than identification.

This Lag RB experiment was similar to the first behavioural experiment, except we also manipulated the temporal 'Lag' between C1 and C2 (2, 3, 5 or 7 items). Each RSVP stream consisted of three intact scenes (C1, distractor, C2) and twelve scrambled scenes. C1 and the distractor scene always appeared at the sixth and seventh serial positions, respectively. C2 would appear immediately following the distractor scene (Lag 2), or after one (Lag 3), three (Lag 5) or five (Lag 7) intervening items. The Lag 2 condition had the same temporal gap between C1 and C2 that was used in the Long ITI RB experiment and reflects the condition in which the RB deficit is most severe (e.g., Kanwisher, 1987; Park & Kanwisher, 1994). All scrambled scenes were different. Catch trials were identical to repeat and non-repeat trials, except C2 was replaced with a scrambled scene, meaning that only two intact scenes were presented. As this version of the RB paradigm was not used with fMRI, we removed the timed response window and long ITI. Participants responded when prompted at the end of the stream. There were 12 practice trials and 6 blocks of 50 test trials.

fMRI Experiment

In the fMRI experiment, we used the Long ITI RB paradigm to manipulate the conditions under which temporal individuation occurred. BOLD activity in response to this task was measured across the whole brain, with a focus on a set of lower- and higher-level *a priori* regions of interest (ROIs; see below). This paradigm included 200 trials split over 8

event-related runs, with 80 repeat, 80 non-repeat and 40 catch trials. Each run consisted of a 20 s fixation period, followed by 25 RB trials and then a 12 s fixation period. Participants responded by pressing one of two buttons on a button box in their right hand for repeat and non-repeat responses, and one button with their left hand for catch responses. The order of trial types was random and the number of trials for each condition was equal across runs.

Localiser task. After the RB runs, participants completed the localiser task. Here, participants were presented with separate 20 s blocks of fixation, face and scene stimuli. At the beginning of each stimulus block, a visual cue was presented for 2 s to indicate the block type. Each block included nine trials in which an intact scene or face was presented for 1 s, followed by a 1 s ITI. On half the scene and face blocks, participants were cued to passively view the stimuli (Passive Scene and Passive Face). On the remaining blocks, participants were cued to classify the scenes as indoor or outdoor scenes (Task Scene) or the faces as male or female (Task Face). This response was speeded and was made using one of two buttons on a response box in their left or right hand, respectively.

There were two localiser runs where each consisted of four blocks of fixation and three blocks of each of the stimulus block types. The order of the stimulus blocks was random without replacement and a fixation block was presented after every four stimulus blocks. An additional 8 s fixation period was presented at the start and end of each localiser run.

Data acquisition. Images were acquired using a 3T Siemens Trio MRI scanner (Erlangen, Germany). Participants lay supine in the scanner and viewed the visual display via rear-projection onto a mirror mounted on a 12-channel head coil. A T1-weighted anatomical image was collected in the middle of the scanning session using an MPRAGE sequence (TR = 1.9 s, TE = 2.32 ms, flip angle = 9º, FOV = 192 x 230 x 256, resolution = 1 mm^3). Functional T2*-weighted images were acquired parallel to the AC-PC plane using a GRE EPI sequence (TR = 2 s, TE = 25 ms, flip angle = 90º, FOV = 192 x 192, matrix = 64 x 64, in-plane resolution = 3 x 3 mm). Each volume consisted of 33 slices (thickness = 3 mm, inter-slice gap = 0.3 mm), providing whole-brain coverage. We synchronised the stimulus presentation with the acquisition of functional volumes. There were 166 and 168 volumes (including 4 dummy volumes) acquired for each of the event-related and localiser runs, respectively.

Data analyses. We analysed our data using Brain Voyager QX software (Brain Innovation, Maastricht, Netherlands) and custom MATLAB code.

Preprocessing. Data preprocessing included 3D motion correction (where each functional image was aligned to the first run), slice-scan time correction and high-pass temporal filtering (3 cycles per run). All functional images were co-registered to the anatomical scan and transformed into standardised space (Talairach & Tourmoux, 1988). No spatial smoothing was applied to preserve fine-grained spatial information for the multi-voxel pattern analyses (MVPA; see below).

Regions of interest. We first isolated a group of 20 ROIs (see Table 1). These regions consisted of perceptual areas involved in processing scenes (parahippocampal place area, PPA; Epstein, Graham, & Downing, 2003) and objects (lateral occipital complex, LOC; Kourtzi & Kanwisher, 2001), regions previously implicated in object individuation and identification (see, Xu, 2009), and higher-level attentional/executive areas associated with capacity limits of information processing (Dux, Ivanoff, Asplund, & Marois, 2006; Dux et al., 2009; Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Jiang & Kanwisher, 2003; Marois, Larson, Chun, & Shima, 2006; Schubert & Szameitat, 2003; Szametitat, Schugbert, Muller, & von Cramon, 2002). Given the extensive overlap between the superior parietal lobule and superior IPS ROIs in the majority of subjects, we collapsed univariate and multivariate results across these two parietal regions (denoted as sIPS/SPL); hence, 18 ROIs were examined.

Table 1. Anatomical locations of the regions of interest.

All regions were isolated using data from the Localiser task. 'Attentional/executive' and 'Object perception' regions of interest (ROIs) were isolated by contrasting activity between stimuli blocks with fixation. The 'Scene perception' ROIs were localised by contrasting activity between scene and face stimuli blocks. The 'No. of Participants' column represents the number of participants for whom an ROI was successfully identified. The 'Talairach Coordinates (x, y, z)' column represents the mean Talairach for each brain region with standard deviation in the parentheses. Region abbreviations are: IFJ, inferior frontal junction; ACC, anterior cingulate cortex; SMFC, superior medial frontal cortex; DLPFC, dorsal lateral prefrontal cortex; PMC, premotor cortex; SPL, superior parietal lobule; sIPS, superior intra-parietal sulcus; iIPS, inferior intra-parietal sulcus; LOC, lateral occipital complex; PPA, parahippocampal place area. L, left; R, right; Bi, bilateral.

ROI	No. of Participants	Talairach Coordinates (x, y, z)
Attentional/executive		
IFJ (L)	18	-43 (2.4), 8 (2.6), 29 (3.1)
(R)	20	44 (5.0), 8 (2.9), 28 (2.4)
ACC (Bi)	22	1 (6.7), 11 (3.7), 39 (2.9)
SMFC (Bi)	23	-2 (4.2), -3 (4.1), 57 (2.4)
DLPFC (L)	19	-33 (3.7), 31 (6.1), 29 (4.8)
(R)	15	37 (5.1), 30 (2.6), 28 (4.6)
PMC (L)	21	-27 (3.9), -8 (3.2), 50 (4.9)
(R)	21	30 (4.4), -6 (4.1), 48 (3.6)
SPL (L)	21	-27 (2.8), -56 (3.6), 44 (3.1)
(R)	21	26 (3.0), -58 (3.8), 45 (3.1)
Insula (L)	19	-33 (4.3), 16 (5.3), 10 (4.0)
(R)	19	34 (4.4), 18 (4.6), 8 (4.0)
Object perception		
Inferior IPS (L)	22	-28 (4.1), -78 (6.2), 25 (4.7)
(R)	22	27 (4.0), -77 (3.7), 25 (4.0)
Superior IPS (L)	23	-26 (3.7), -62 (2.8), 40 (3.8)
(R)	23	26 (3.7), -56 (4.9), 44 (3.1)
LOC (L)	23	-34 (3.2), -80 (3.4), 13 (3.1)
(R)	22	46 (3.9), -59 (4.2), 4 (4.4)
Scene perception		
PPA (L)	23	-24 (2.1), -42 (2.3), -6 (1.7)
(R)	23	24 (1.9), -42 (1.7), -6 (1.6)

To localise these ROIs in each participant, we submitted data from the localiser runs to single-participant general linear model voxel-wise analyses using a statistical threshold of $q < .05$ (FDR). We defined regressors for the Fixation, Passive Face, Task Face, Passive Scene and Task Scene blocks, which were then convolved with a double-gamma hemodynamic response function. To isolate the PPA, we contrasted activity between scene and face blocks. Bilateral PPA ROIs were identified as active voxels in the anterior section of the parahippocampal gyrus in the left and right hemisphere (Epstein et

al., 2003). To isolate the remaining ROIs, we contrasted activity in the four stimulus blocks with Fixation. We defined the object perception and attentional/executive ROIs on these statistical maps using mean Talairach coordinates derived from Xu (2009) and Dux et al. (2009), respectively, as a guide for establishing the most relevant functionally-defined regions. Each ROI was identified as the cluster of active voxels that most closely matched the previously established coordinates for that region. If there were two non-contiguous equidistant activation clusters, we used whichever cluster was still present at a more stringent threshold. In each region, we only analysed data from the event-related runs for participants in which that ROI could be isolated (see Table 1).

For the univariate analysis, an ROI included all voxels above statistical threshold surrounding the peak voxel up to a maximum of 6 x 6 x 6 mm (8 voxels). For the multivariate analysis, ROIs were defined by a 15 x 15 x 15 mm and 21 x 21 x 21 mm cube (125 and 343 voxels, respectively), centered on each individual participant's Talairach coordinates of the peak voxel. We used larger ROI sizes in the multivariate analysis to increase variance across voxels and be consistent with other studies that have employed this analytic technique (e.g., Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011; Harrison & Tong, 2009; Kamitani & Tong, 2005; Oosterhof, Tipper, & Downing, 2012). We defined ROIs for the multivariate analyses using two different sizes to ensure that decoding results were reliable, regardless of the particular number of voxels included in the analysis (Spiridon & Kanwisher, 2002). We only report the MVPA results for ROIs defined by a 21 x 21 x 21 mm cube, but our findings were consistent across both ROI sizes unless otherwise stated.

Univariate analysis. We first analysed data from the RB event-related runs using a standard univariate approach. Timecourses for each condition, ROI (with signal averaged across all voxels in the ROI) and participant were extracted. Percentage signal change was calculated relative to signal during the volume preceding trial onset. This baseline was chosen to exclude any potential activity associated with the previous trial. Individual participant timecourses were averaged across all participants and we compared differences in peak amplitude between the experimental conditions. Peak amplitude was defined as the averaged signal across time points 4-8 s post-trial onset. Statistical significance was assessed using repeated-measures *t*-tests and a statistical threshold of $p < .05$ (Bonferroni corrected for the 18 regions tested).

Multivariate analyses. To increase the sensitivity of our analysis, we also analysed our data using MVPA (Haynes & Rees, 2006; Kamitani & Tong, 2005). This analytic approach is more sensitive than univariate methods as it examines differences in activity

across multiple voxels, rather than each voxel individually. Indeed, activity within any single voxel might show weak differences between conditions if only a small proportion of neurons in that voxel code for information associated with the experimental task. MVPA attempts to improve the sensitivity of fMRI analysis by pooling these weak, but reliable, signals across voxels and comparing conditions based on the resulting ensemble patterns of activity. MVPA was implemented using custom MATLAB software and a linear support vector machine binary algorithm (Chang & Lin, 2011).

For each voxel in a given ROI, we extracted the average percentage signal change corresponding to the peak of the timecourse for each trial (4-8 s post-trial onset). Before each MVPA, data for each voxel in an ROI were z-transformed and mean-centered by subtracting the condition mean for the entire ROI from the response in each individual voxel to control for overall differences in signal amplitude between conditions (see, Esterman, Chiu, Tamber-Rosenau, & Yantis, 2009; Tamber-Rosenau, Esterman, Chiu, & Yantis, 2011). We trained a series of binary classifiers to discriminate between patterns of activity associated with the experimental conditions using the leave-one-out cross-validation method. In each fold, one run was used to test the classifier's generalisation performance and the remaining seven runs were used to train the classifier. Decoding accuracy for each ROI was averaged across each cross-validation loop and tested against chance accuracy (50%) using one-sample *t*-tests and a statistical threshold of $p < .05$ (Bonferroni corrected for the 18 regions tested). If there is a functional distinction between pools of neurons within a given ROI that respond to each condition, then the classifier should be better than chance at discriminating between patterns of activity on the test trials (Pereira, Mitchell, & Botvinick, 2009).

We also performed a searchlight analysis to explore whether other regions outside our ROIs showed a similar pattern of results to the ROIs we tested (Kriegeskorte, Goebel, & Bandettini, 2006). A spherical searchlight ROI with a 2-voxel radius (33 voxels) was centered on every voxel of the volume. We used the same cross-validation classification method procedure as the ROI analysis to test for information contained in these local activity patterns. Classification accuracy for each searchlight was assigned to the central voxel and compared against chance performance to test for significance ($q < .05$, FDR).

Results

All statistical analyses were conducted with a two-tailed alpha level of .05 and a Bonferroni correction was applied for multiple comparisons unless otherwise stated.

Behavioural Experiments

Chance performance in the RB task was 33.3%. To first assess whether our paradigm could elicit the standard RB behavioural effect, we submitted the mean detection accuracy data from the Long ITI RB experiment to a repeated-measures *t*-test. Detection accuracy reflects the percentage of trials in which participants correctly detected the identity of the two critical scenes (e.g., a 'repeat' response on repeat trials; 'non-repeat' or 'two scene only' responses would be considered incorrect on this trial). Consistent with other RB studies that have used a similar paradigm to ours (e.g., Hochhaus & Johnston, 1996; Kanwisher et al., 1996; Park & Kanwisher, 1994), participants were significantly less accurate on repeat trials relative to non-repeat trials, $t(5) = 2.93$, $p = .033$ (see Figure 2A). In subsequent experiments conducted in our laboratory, we have replicated this RB result using alphanumeric stimuli, suggesting that this behavioural effect is not specific to the type of stimulus used. Performance on catch trials was around chance in this experiment ($M = 36.7\%$, $SD = 8.2\%$), $t(5) < 1$, where participants' erroneous responses were more likely to be a non-repeat response than a repeat response (69.6% versus 25.2% of errors, respectively; the remaining 5.2% of errors were absent responses). This proportion and pattern of catch trial errors is consistent with previous RB studies (Dux & Coltheart, 2008).

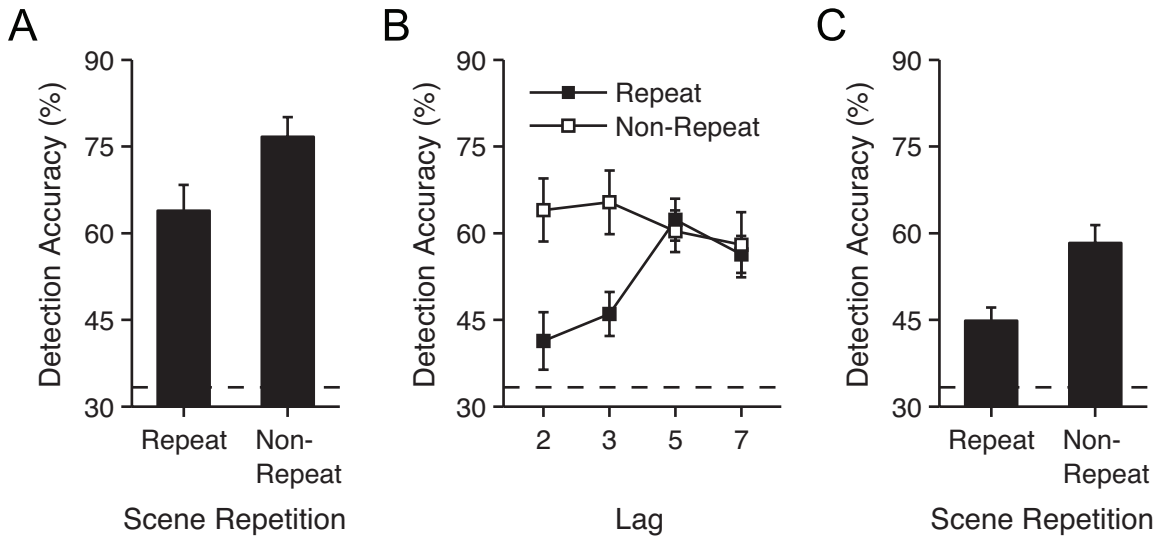

Figure 2. Behavioural results from the behavioural and fMRI experiments.
(A) Mean detection accuracy results from the Long ITI RB experiment, separately for repeat and non-repeat trials. (B) Mean detection accuracy from the Lag RB experiment, separately for repeat and non-repeat trials across the four temporal lag conditions. (C) Mean detection accuracy results from the fMRI experiment, separately for repeat and non-

repeat trials. Error bars represent one standard error of the mean across participants and the dotted line indicates chance performance (33.3%).

Data from the Lag RB experiment were used to test whether our RB paradigm specifically tapped the temporal capacity limits of individuation, rather than identification. If our paradigm elicited identification limitations, we expected participants would be poorer at detecting both repeated and non-repeated scenes at shorter temporal lags, relative to longer temporal lags. On the other hand, deficits in individuation indicate a specific difficulty in registering two repeated items as separate stimuli. Thus, if our paradigm only tapped the temporal capacity limits of individuation, we predicted detection of repeated scenes alone would be affected by lag.

To assess this, we submitted mean detection accuracy data from the Lag RB experiment to a 2 (Scene Repetition: repeat, non-repeat) by 4 (Lag: 2, 3, 5, 7) repeated-measures ANOVA. A significant main effect was found for both Scene Repetition, $F(1, 9) = 5.51$, $MSE = 394$, $p = .044$, $\eta_p^2 = .38$, and Lag, $F(3, 27) = 4.44$, $MSE = 75$, $p = .012$, $\eta_p^2 = .33$ (see Figure 2B). Crucially, a significant interaction between these two factors also emerged, $F(3, 27) = 6.28$, $MSE = 169$, $p = .002$, $\eta_p^2 = .41$. Follow-up *t*-tests revealed detection accuracy on repeat trials was significantly reduced at shorter lags (Lags 2 and 3) relative to longer lags (Lags 5 and 7), $t(9) = 5.55$, $p < .001$, but detection accuracy on non-repeat trials did not vary with Lag, $t(9) = 1.31$, $p = .222$. Thus, our RB paradigm specifically tapped temporal capacity limitations associated with individuation rather than identification. These findings demonstrate that the present paradigm elicited a pure RB effect that was not confounded by the AB. Similar to the first behavioural experiment, catch trial performance was no greater than chance ($M = 24.5\%$, $SD = 16.2\%$), $t(9) = 1.72$, $p = .119$.

fMRI Experiment

Behavioural performance. A repeated-measures *t*-test revealed that behavioural performance on the RB task inside the scanner was consistent with previous behavioural experiments, whereby detection accuracy was reduced on repeat trials relative to non-repeat trials, $t(22) = 4.72$, $p < .001$ (see Figure 2C). In contrast to the behavioural experiments, however, performance on catch trials was significantly above chance ($M = 46.4\%$, $SD = 5.0\%$), $t(22) = 2.67$, $p = .014$, with participants more likely to make erroneous non-repeat than repeat responses (54.0% versus 27.1% of errors, respectively; the remaining 19.0% of errors were absent responses). Participants could successfully

complete the task blocks on the Localiser runs as behavioural performance was close to ceiling (*M*s > 93.0 %, *SD*s < 1.2 %), *t*s > 36.06, *p*s < .001 (compared to chance).

Trial types and comparisons. For the fMRI analyses, we binned repeat and non-repeat trials into the following conditions: Hit (repeat trial, repeat response), Miss (repeat trial, non-repeat response), Correct Rejection (non-repeat trial, non-repeat response) and False Alarm (non-repeat trial, repeat response). Table 2 displays the average response proportions for all conditions. Note that catch trials (or repeat/non-repeat trials where a 'two scene only' response or no response was made) were not included in the fMRI analyses as these trials served only as filler trials to reduce the likelihood of guessing responses.

Table 2. Average response proportions to repeat, non-repeat and catch trials in the fMRI experiment.

	Response				
Trial Type	Repeated	Non-Repeated	Catch	Absent	Total
Repeat	0.45 (0.11)	0.25 (0.10)	0.05 (0.04)	0.26 (0.13)	1.00
Non-Repeat	0.14 (0.14)	0.58 (0.15)	0.10 (0.08)	0.18 (0.11)	1.00
Catch	0.11 (0.09)	0.28 (0.13)	0.46 (0.23)	0.15 (0.10)	1.00

To first isolate the brain areas involved in temporally individuating items during encoding, we compared Hit and Correct Rejection trials as these conditions place different demands on individuation. That is, given that repeated stimuli presented in close temporal proximity are more difficult to individuate relative to non-repeated stimuli (Kanwisher, 1987), Hit trials should, on average, place greater demands on the process of temporal individuation, relative to Correct Rejection trials. It is important to note that this comparison reflects only trials on which a correct response was made, and we therefore know, with some degree of certainty, that the scenes were successfully individuated in both trial types (although this process was more demanding in under Hit trials). In addition, this comparison is balanced in terms of reward associated with making a correct response. Our second key comparison aimed to identify brain areas involved in the RB deficit (i.e., regions that may underlie the capacity limit on temporal individuation). To do this, we contrasted Hit and Miss trials, as this comparison reflects instances where two repeated stimuli are successfully detected or not. As RB reflects an inability to bind a second repeated item's identity to its token, rather than a failure to create the second token

altogether (Kanwisher, Driver, & Machado, 1995; Kanwisher, 1987; Park & Kanwisher, 1994), it was more appropriate to compare between conditions that reflect a misidentification error, rather than trials where participants reported seeing nothing at all (e.g., Hits versus Repeated scene/'Two scene only' response trials). Even though this RB comparison uses trial definitions that are based on a post-run selection of trials by accuracy, this is a common approach employed in imaging studies that use RSVP tasks (e.g., Marois et al., 2004). We tested for differences using both univariate gross amplitude and multivariate spatial patterns of BOLD activity.

Univariate analyses. For the demands on temporal individuation comparison, we found no significant amplitude differences between Hit and Correct Rejection trials. This finding suggests that the amplitude of activity in all of our ROIs was not modulated by conditions that place differential demands on temporal individuation. On the other hand, when we compared between conditions that reflect a capacity limit of temporal individuation, we found a single region – left hemisphere premotor cortex – that showed significantly greater activity on Miss trials relative to Hit trials, $t(20) = 3.42$, $p = .049$ (corrected for multiple comparisons, see Figure 3). Thus, processing in this region may be involved in RB.

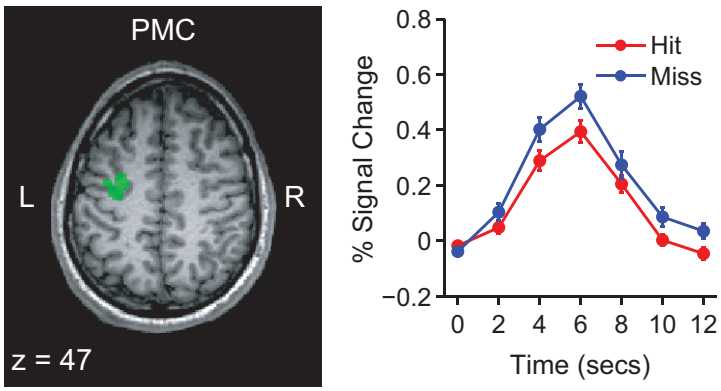

Figure 3. The single significant region of interest that reflected changes in gross blood oxygen level dependent amplitude for the capacity limits of temporal individuation.

Anatomical images show individual regions of interest (ROIs) from all participants for whom an ROI could be identified for that given area. As none of the ROIs showed significant differences in blood oxygen level dependent (BOLD) amplitude between Hit and Correct Rejection trials (demands on temporal individuation comparison), the graphs only display BOLD timecourse for Hit and Miss trials for this region. Error bars denote one

standard error of the mean across participants. Peak amplitude was taken as the average signal across volumes 4-8 s post-trial onset. Region abbreviations are the same as Table 1.

These gross differences in BOLD amplitude were specific to the successful individuation of two repeated stimuli, as none of our ROIs showed any differences in amplitude between correct and incorrect non-repeated trials (Correct Rejections versus False Alarms, *t*s < 2.16, corrected for multiple comparisons *p*s > .809). This result is consistent with behavioural findings from the Lag RB experiment in that it shows that our paradigm specifically taps processing limitations associated with the perception of two repeated stimuli, but not two non-repeated stimuli (see also, Chun, 1997). In addition, this difference in amplitude cannot simply reflect response conflict or ambiguity, as this same region responded similarly on Hit and False Alarm trials, $t < 1$. These trial types showed the greatest difference in reaction time (1166 ms versus 1430 ms; although response speed was not emphasized in the task) and would arguably reflect the greatest difference in response uncertainty.

Multivariate analyses. We further explored the neural underpinnings of temporal individuation and its capacity limits using ROI-based and whole-brain searchlight MVPAs. As our experimental conditions were jointly determined by stimulus presentation and participants' response, the number of trials in each condition was not balanced. Unbalanced trials are particularly problematic for MVPA as this can bias the classifier towards the more numerous condition, rather than the actual properties associated with the experimental conditions (Pereira et al., 2009). To address this issue, we balanced trial numbers across conditions in both training and testing subsets by removing a random selection of trials from the more plentiful condition before the MVPA. Decoding results for the ROI-based MVPA were averaged across 100 repetitions of this procedure and the number of iterations was reduced to 10 for the searchlight analysis to save computation time. Using this strict balancing method, there was an average of 35 trials in training sets and 5 trials in testing sets in each cross-validation loop.

ROI-based MVPA. To first identify differences in activity patterns associated with the demands placed on temporal individuation, we trained a classifier to discriminate between Hit and Correct Rejection trials in each of our ROIs. Above-chance decoding performance for this comparison emerged in 17 out of our 18 ROIs, *t*s > 4.22, *p*s < .010 (corrected for multiple comparisons, see Figure 4). While activity in the left hemisphere dorsolateral prefrontal cortex (DLPFC) could be discriminated between these two

conditions for the 21 mm ROI cube, this result did not hold for the 15 mm ROI cube, $t(18) = 2.28$, $p = .637$. The significant ROIs included both lower-level areas involved in perceptual processes (e.g., Epstein et al., 2003; Kourtzi & Kanwisher, 2001; Xu, 2009) and higher-level executive areas that have previously been associated with other capacity-limited processes, such as response selection, decision making and encoding (e.g., Dux et al., 2006; Dux et al., 2009; Heekeren et al., 2004; Szametitat et al., 2002; Tombu et al., 2011). In contrast, the classifier was only able to differentiate between activity patterns associated with successful and unsuccessful instances of temporal individuation (Hits versus Misses) in the left hemisphere superior IPS/SPL, $t(21) = 3.58$, $p = .031$ (corrected for multiple comparisons). This result, however, did not hold over changes in ROI size (classification under 15 mm ROI cube, corrected for multiple comparisons $p > 1$). These multivariate results therefore suggest that perceptual demands placed on temporal individuation influence the patterns of activity across a widely distributed set of brain regions, including both lower and higher cortical areas. This finding contrasts with the single brain region that has previously been associated with spatial individuation (Xu, 2009) in that it suggests that this process is underpinned by a far more distributed set of areas. The processing limitations associated with individuation, however, have no consistent effect on the ensemble patterns of activity in any region.

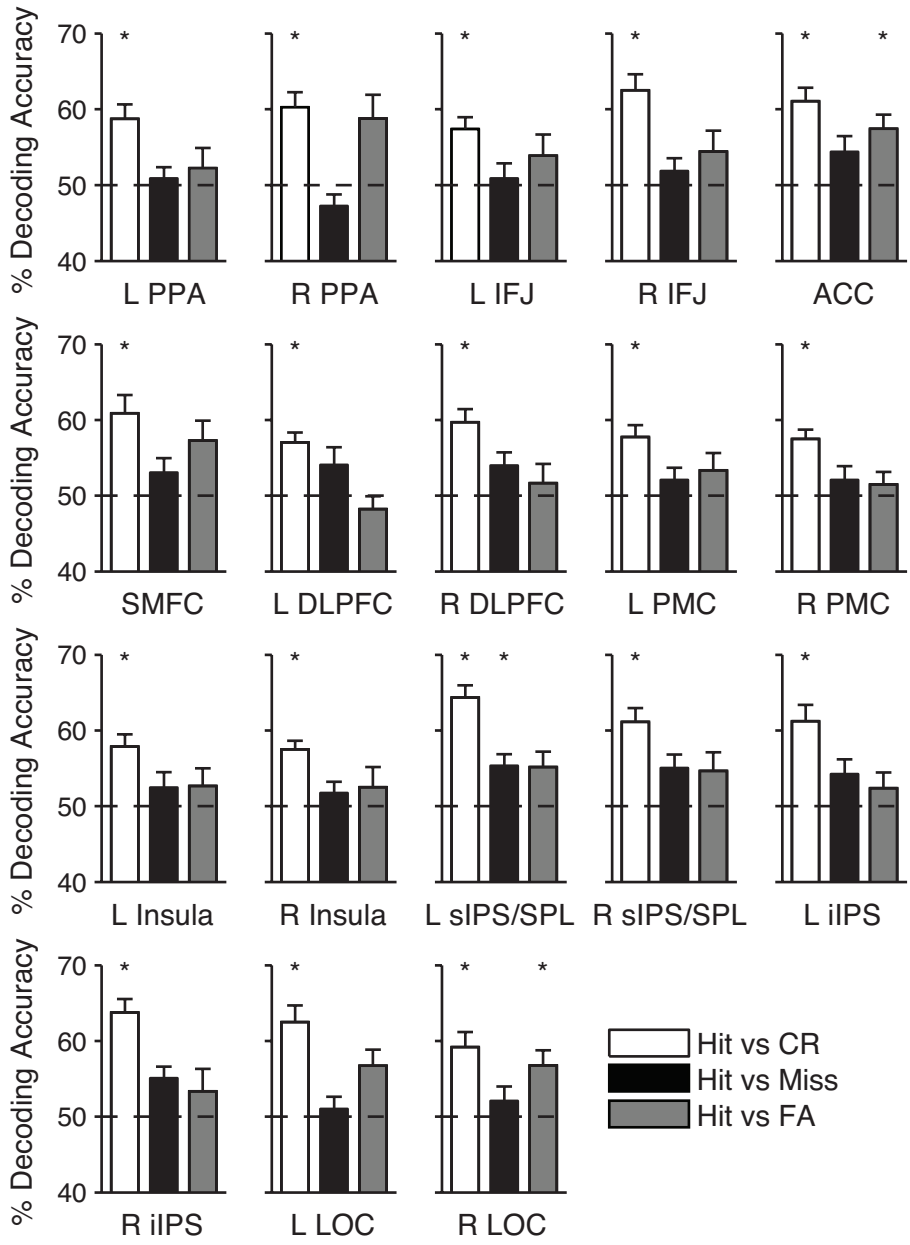

Figure 4. Results from the main multivariate analyses and task difficulty control analysis.

The Hit versus Correct Rejection (CR) comparison reflected differences in the demands placed on temporal individuation (denoted by the white bars). The Hit versus Miss comparison identified the neural consequences associated with the capacity limits of temporal individuation (denoted by the black bars). The Hit versus False Alarm (FA) comparison reflected reaction time differences as a proxy for task difficulty-related changes in activity patterns (denoted by grey bars). Chance performance is indicated by the dotted line and the significance symbol (*) reflects greater than chance performance at

$p < .05$ (corrected for multiple comparisons). Error bars represent one standard error of the mean. Region abbreviations are the same as Table 1.

Control analyses. We conducted an additional set of control MVPAs to test whether the distributed differences in activity patterns associated with Hit and Correct Rejection trials were driven by other differences that existed between these conditions (i.e., not related to individuation). As Hit and Correct Rejection trials showed significant differences in reaction time (1166 versus 1297 ms, $t(22) = 4.23$, $p < .001$), the first control analysis aimed to assess whether our results could be attributed to task-related effects such as general difficulty or the amount of time spent on the task. Using reaction time as a proxy for task difficulty, we trained classifiers to discriminate between the two trial types that showed the largest difference in reaction time: Hit (1166 ms) and False Alarm trials (1430 ms), $t(22) = 5.50$, $p < .001$. Significant decoding emerged for this comparison in the anterior cingulate cortex (ACC) and right hemisphere LOC, ts > 3.46, ps < .042 (corrected for multiple comparisons), however only the ACC result was also observed for the 15 mm cube (ACC, $t(21) = 3.94$, $p = .014$; right hemisphere LOC, $t(21) = 2.96$, $p = .134$). Results from this control analysis suggest that, with the possible exception of the ACC, the distributed patterns of activity associated with the perceptual demands placed on temporal individuation do not simply reflect task difficulty or the amount of time spent on the task. In contrast to the remaining ROIs, the activity patterns in the ACC likely reflect general task difficulty as opposed to a specific difficulty associated with individuating two scenes. Further, the lack of significant results are unlikely to reflect insufficient power due to the low number of False Alarm trials, as our results from the demands on temporal individuation comparison held for all previously significant ROIs (ts > 3.29, $p = .078$ for left hemisphere inferior frontal junction, ts > 3.48, ps < .048 for all other ROIs, both corrected for multiple comparisons) even when we equated trial numbers across all trial types, rather than only across the conditions being compared.

The second set of control analyses tested whether the differences in activity patterns associated with temporal individuation reflected purely stimulus- or response-related effects, as Hit and Correct Rejection conditions differed on both these factors. To first test for stimulus-related differences in activity, we decoded patterns of activity associated with repeated and non-repeated stimuli, regardless of participants' response. For this analysis, we collapsed across both repeated stimuli (Hits and Misses) and non-repeated stimuli (Correct Rejections and False Alarms) conditions to give ourselves the best chance of detecting any stimulus-related effects if they did indeed exist. As we used

all four trial types in this analysis, we balanced trial numbers across all conditions prior to decoding to ensure the differences in trial numbers did not affect the results. No significant decoding emerged for repeated and non-repeated stimulus conditions in any region, *t*s < 2.97, *p*s > .126 (corrected for multiple comparisons, see Figure 5), suggesting that none of our ROIs exclusively coded for stimulus properties in this experiment.

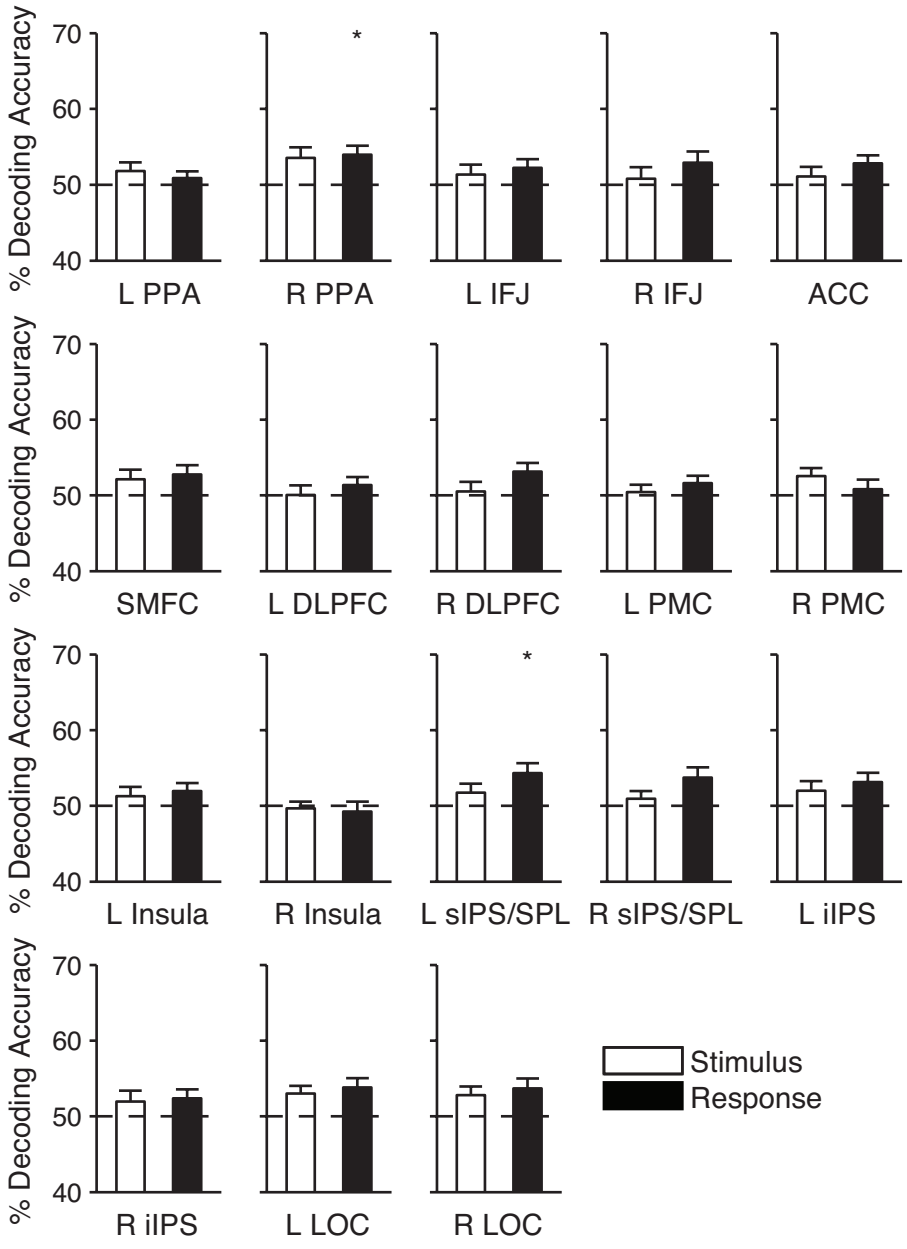

Figure 5. Results from the stimulus and response multivariate control analyses. This figure is displayed in the same format as Figure 4. To identify purely stimulus-driven changes in activity patterns, we compared repeated and non-repeated stimuli trials, regardless of participants' response (Hit and Miss versus Correct Rejection [CR] and False

Alarm [FA], denoted by white bars). Likewise, to isolate purely response-driven changes in activity patterns, we contrasted instances where participants made a repeated and non-repeated response, regardless of the stimulus presentation (Hit and FA versus CR and Miss, denoted by black bars).

We also decoded activity patterns associated with repeated and non-repeated responses regardless of the stimulus presentation (Hits and False Alarms versus Misses and Correct Rejections), and found these two conditions could be discriminated in two of the eighteen ROIs: The right hemisphere PPA and left hemisphere sIPS/SPL, *t*s > 3.38, *p*s < .048, corrected (see Figure 5). The same decoding performance in these regions did not hold across both ROI sizes, however, suggesting that the response coding in these regions was not reliable (*t*s < 2.80, *p*s > .189, for 15 mm ROI cube). Thus, the widespread differences in patterns of activity associated with Hit and Correct Rejection conditions did not appear to be purely stimulus- or response-based, but rather reflected an interaction between these stimulus and decision/response factors that would be necessary to individuate temporally distinct items.

Although our results were not driven by stimulus and response factors individually, one could argue that they reflect a simple stimulus-response interaction rather than anything specific to temporal individuation. To provide further support that our Hit versus Correct Rejection comparison reflects temporal individuation demands, rather than some other sort of stimulus-response interaction, we decoded Miss versus False Alarm trials (we balanced trial numbers in this comparison as well, like all other analyses). These are both incorrect trials so we cannot be sure of the extent to which each critical item was individuated, but these trials do differ in terms of the stimulus presented and the response made. Unlike our key analysis of Hit versus Correct Rejection, the analysis of Miss versus False Alarm revealed significant decoding in the bilateral LOC only, *t*s > 3.49, *p*s < .039 (corrected). Importantly, after averaging over decoding values in all the ROIs, to increase statistical power and counter the fact that not all subjects showed every ROI (see Table 1), we found that the overall decoding across the brain for Hits versus Correct Rejections was significantly greater than that found for Miss versus False Alarms, $t(22) = 2.91$, $p = .008$ (uncorrected, as data was averaged across all ROIs). Collectively, these results suggest all significant Hit versus Correct Rejection ROIs – with the possible exception of the bilateral LOC – reflect the specific stimulus-response interaction involved in temporal individuation. As we elaborate on in the General Discussion, we propose that such interactions are facilitated within a distributed neural framework or ‘workspace’ in which

information can be shared between lower and higher regions (Baars & Franklin, 2003; Dehaene et al., 2003; Sergent & Dehaene, 2004).

A final control analysis was conducted to ensure that results from the demands on temporal individuation analysis did not simply reflect a data artifact that would produce above chance decoding across the entire brain. To test this, we decoded activity patterns in two additional control ROIs that predominantly respond to auditory information rather than visual information (left and right primary auditory cortices). These ROIs were anatomically defined as the superior region of the temporal lobe (Rademacher et al., 2001). We decoded activity in these areas for the two main comparisons and the task difficulty control comparison. If decoding performance in the temporal individuation analysis did indeed reflect the differential perceptual demands associated with individuating visual stimuli across time (and not an artifact in the data, task design, or analysis), the classifier should be no better than chance at discriminating between Hit and Correct Rejection conditions in either of these control regions. Consistent with this prediction, no significant decoding emerged in either of the auditory ROIs for any of the classifier comparisons, including the demands on temporal individuation comparison, *t*s < 2.32*, p*s > .544, corrected for multiple comparisons (see Figure 6).

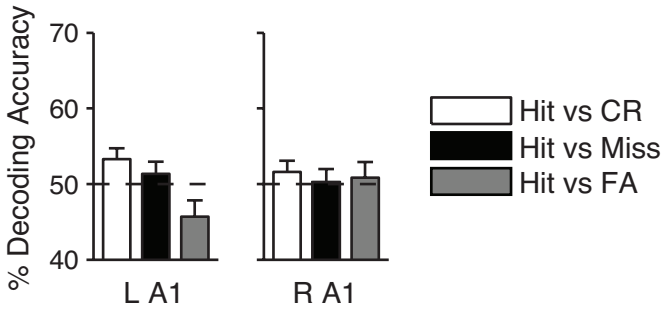

Figure 6. Results for the main and task difficulty control multivariate analysis for the two control regions.

This figure is displayed in the same format and reflects the same comparisons as Figure 4. Region abbreviations are: A1, primary auditory cortex; L, left; R, right.

Searchlight analysis. We conducted a whole-brain searchlight analysis to determine if brain regions other than our ROIs could discriminate between the different demands placed on temporal individuation. Consistent with our previous ROI-based MVPA, the searchlight analysis revealed that widespread parts of the brain show distinct activity patterns for Hit compared to Correct Rejection trials (see Figure 7). The information

map generated from this analysis included all of our ROIs, and provided confirmatory support for the findings that emerged in our ROI-based MVPA. In addition to these ROIs, we also found that large parts of the frontal, parietal and occipital cortices were sensitive to the conditions under which temporal individuation occurred. Consistent with our control ROI analysis, no voxels in the auditory cortices could be reliably classified, suggesting that our classification results do not reflect an artifact of the data analyses. We also performed a searchlight analysis for the RB comparison, but found no significant classification across the entire brain. This finding further supports the idea that the processing limitations that lead to RB modulate the amplitude, rather than the patterns, of BOLD activity.

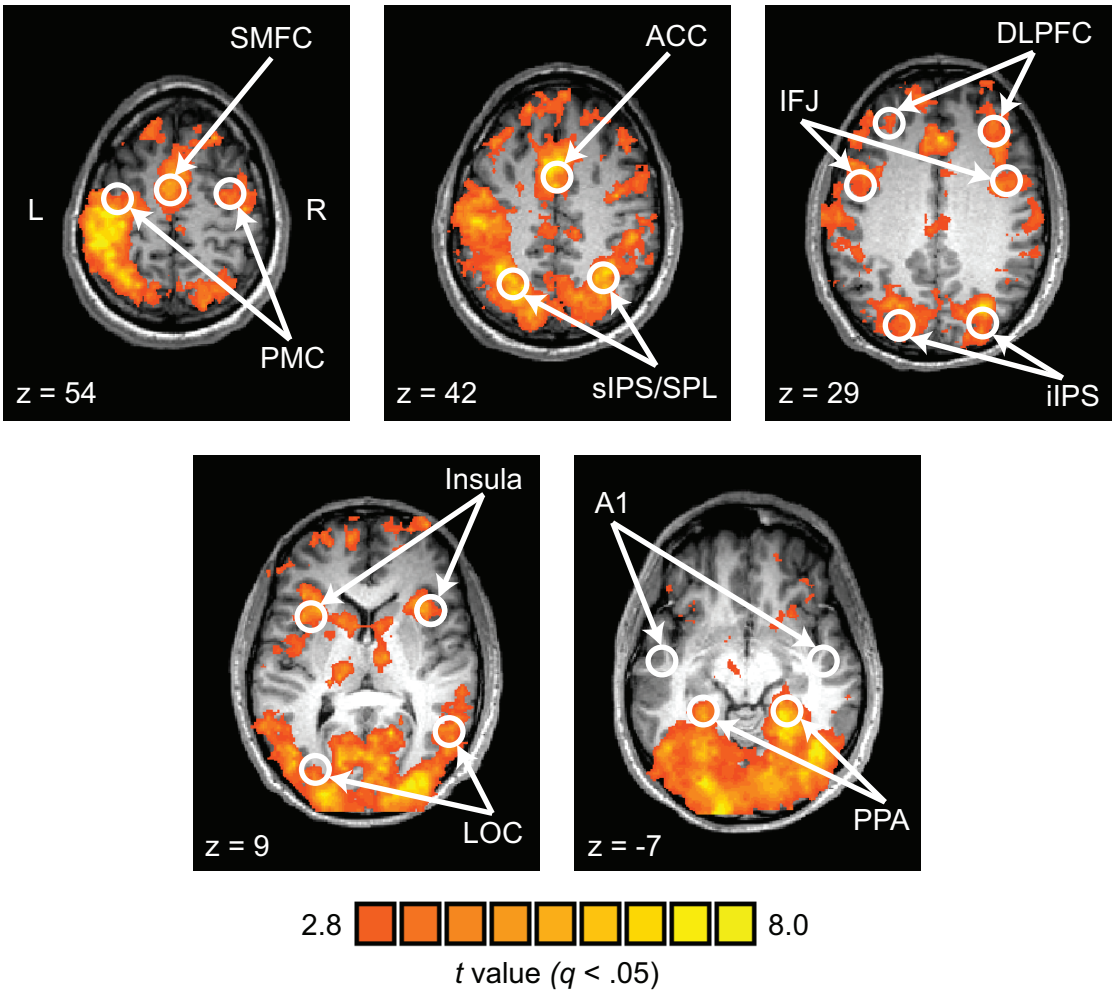

Figure 7. Results for the whole-brain searchlight analysis for the demands on temporal individuation comparison.

We centered a searchlight ROI (33 voxels) on every voxel in the volume and tested for differences in these local patterns for Hits versus Correct Rejections. Classification accuracies were compared to chance performance (50%) and *t*-values are only displayed

for voxels that survived the multiple comparisons correction (q < .05). Region abbreviations are the same as Table 1.

General Discussion

The purpose of the present study was twofold: First, we aimed to examine whether individuation processes could be localized to a single neural correlate or if this operation tapped a widely distributed network of brain areas, as has been proposed in models of consciousness and encoding (Baars & Franklin, 2003; Dehaene et al., 2003; Sergent & Dehaene, 2004). Second, we aimed to pinpoint the neural areas involved in the behavioural RB deficit. To accomplish these goals, we employed an RB paradigm and a combination of univariate and multivariate analysis techniques. In response to the first aim, we found that activity patterns associated with the perception of two repeated stimuli (which are more demanding to individuate) and non-repeated stimuli (which are relatively easy to individuate) could be successfully discriminated. Critically, these two conditions reflected correct trials, meaning that we can be confident that stimuli were successfully individuated on these trials, although this process was more demanding for repeated stimuli. Even though these two conditions could not be distinguished when univariate BOLD amplitude was compared, our multivariate analyses revealed that these conditions elicited reliably different spatial patterns of activity in the majority of our ROIs. This set of regions included both lower-level perceptual and higher-level attentional/executive regions that covered parts of the frontal, parietal and occipital cortices. Although we cannot be sure of the stage(s) of processing at which the increased demands associated with temporal individuation had their impact, our findings nevertheless demonstrate a measurable difference in BOLD activity that is evoked by these changes in temporal individuation demands.

For our secondary analysis – to identify the brain area(s) associated with RB (i.e., a processing limitation associated with temporal individuation) – we compared activity between conditions in which two repeated stimuli were successfully detected or not. In contrast to the primary analysis in which we manipulated the demands on temporal individuation, we found that this RB analysis did not reliably affect the spatial patterns of activity in any of our ROIs, but instead modulated the amplitude of BOLD activity in the left hemisphere premotor cortex. Together, our findings suggest that a large group of cortical regions are sensitive to demands placed on the temporal individuation process, whereas the processing limitations associated with this operation that lead to RB specifically influence the strength of activity in a focal brain region. Our two key comparisons therefore

appear to reflect distinct processes: The demand or load associated with constructing an individuated representation across time, and a specific capacity limitation associated with individuation.

The differences that emerged for the amplitude and patterns of BOLD activity resonate with recent findings in the visual short-term memory literature. Several studies have shown that increasing the number of items held in memory leads to sustained, elevated BOLD amplitude in the parietal cortex (Todd & Marois, 2004; Xu & Chun, 2006), yet maintaining these items in memory alters the patterns, but not the amplitude, of activity in early sensory areas (e.g., Emrich, Riggall, LaRocque, & Postle, 2013; Serences, Ester, Vogel, & Awh, 2009). Emrich et al. (2013) suggest that changes in activity patterns in sensory areas reflect the precision of item representations (see also, Ester, Anderson, Serences, & Awh, 2013), whereas changes in amplitude are associated with the allocation of attention resources to a limited number of items. An analogous explanation fits our findings, where the distributed changes in activity patterns associated with the demands placed on temporal individuation could reflect the precision of individuated representations. On the other hand, the specific changes in amplitude reflected by RB could arise from processing limitations associated with the allocation of attentional resources that are necessary to bind an individuated representation (token) to its identity (type).

Decoding associated with the demands placed on temporal individuation was only attributed to a general effect of task difficulty in one ROI (the ACC), as the patterns of activity in the remaining ROIs did not discriminate between differences in reaction time. These remaining regions appear to reflect the demands associated with individuating two temporally distinct scenes, whereas the ACC appears to code for more general task-related effects. The latter finding fits well with the existing literature that suggests that the ACC is involved in general task conflict and cognitive control (Kerns et al., 2004).

Differences associated with temporal individuation were also distinguished from purely stimulus- or response-related effects, as classifiers could not consistently discriminate between repeated and non-repeated stimuli (regardless of participants' response) or responses (regardless of the physical stimulus presentation) in any of our 'temporal individuation' regions. This finding suggests that these brain areas code for the interaction between stimulus and decision/response factors associated with successfully individuating two temporally distinct visual items. Importantly, this stimulus-response interaction appears to be specifically related to temporal individuation in all regions with the possible exception of the bilateral LOC, as it was only in this area where patterns of

activity could distinguish between Miss and False Alarm trials. These trials differed in stimulus and response characteristics but likely not in the demands they placed on temporal individuation. Moreover, when we collapsed decoding results across all ROIs for the Hit versus Correct Rejection comparison and Miss versus False Alarm comparison, we found a significant overall difference between these two comparisons, suggesting that the information reflected by these two comparisons differs across the brain. In addition, signals associated with Hits and Correct Rejections were restricted to brain regions that code for visual information or higher-level abstractions that do not depend on perceptual modality, and our decoding findings did not extend to other non-visual (auditory) areas. Thus, activity patterns associated with the differential demands placed on temporal individuation did not merely reflect false positives across the entire brain. Finally, our key individuation results cannot reflect general positive effects of target detection (e.g., reward, satisfaction), as both Hits and Correct Rejections represent correct trials and would presumably have elicited the same level of reward and satisfaction.

In contrast to the wide set of brain areas that emerged in the current study, previous research and theoretical models of object individuation have attributed this operation to a single brain region (see, Jeong & Xu, 2013; Xu, 2009; Xu & Chun, 2006, 2007, 2009). Studies such as those by Xu and colleagues are not uncommon in the cognitive neuroscience literature and assume that any given perceptual or cognitive process will be supported by a focal set of brain areas. Although this approach is hypothesis-driven, it can be problematic as it limits the underlying neural substrates associated with particular processes, and might miss the involvement of a more diffuse network of brain regions (see, Vickery, Chun, & Lee, 2011). For example, it was previously thought that signals associated with reward processes were represented in specific parts of the basal ganglia, prefrontal and parietal cortex (Elliott, Friston, & Dolan, 2000; Kable & Glimcher, 2007; Kahnt, Heinzle, Park, & Haynes, 2010; Rushworth & Behrens, 2008; Vickery & Jiang, 2009). More recently however, Vickery et al. (2011) used MVPA to show that reward processes are reflected across the whole brain, suggesting that cognitive operations (like temporal individuation studied here) can be underpinned by an extensive neural network. Interestingly, these authors identified only a small subset of areas involved in reward processing when they employed a univariate approach.

The widespread patterns of activity that emerged for temporal individuation are instead in line with existing accounts of consciousness, such as the global neuronal workspace model (Dehaene et al., 2003; Sergent & Dehaene, 2004; see also, Baars & Franlin, 2003). According to this framework, conscious awareness is underpinned by a

distributed network of *workspace neurons* that communicate via long-range connections in the brain. For a stimulus to be consciously perceived, it must activate this workspace, which then allows information to be accessed by a wide variety of processes. The global neuronal workspace model hypothesizes that these neurons are present in both early sensory areas and higher-level parietal and frontal areas, and information about a given stimulus is transferred through recurrent communications between different levels of the cortical hierarchy. In the context of the present study, these long-range connections provide a possible avenue in which lower and higher cortical areas interact during temporal individuation. We hypothesize that conditions in which it is more demanding to individuate two distinct object occurrences alter communications within this distributed workspace, leading to changes in the resulting patterns of activity in both lower- and higher-level brain areas. Our findings provide important insights into the neural underpinnings of temporal individuation in that we show it is a far more distributed process in the brain than initially proposed (e.g., Xu, 2009; Xu & Chun, 2009).

It is interesting to consider the discrepancy between the results we report here and those from prior investigations into individuation by Xu and colleagues (Jeong & Xu, 2013; Xu, 2009; Xu & Chun, 2006, 2007). These previous studies implicated the inferior IPS as the sole substrate of object individuation, which contrasts with the more diffuse group of brain regions we found in the current work. Even when we analysed our data using the same univariate method as Xu and colleagues, we found that BOLD activity in a smaller group of ROIs was modulated by the demands placed on temporal individuation (ACC, superior medial frontal cortex, left hemisphere DLPFC and left hemisphere LOC, ts > 2.18, ps < .043, using the uncorrected test as in Xu and colleagues), but this subset did not include the inferior IPS. Below we consider several key differences between these previous studies and our work that could account for this discrepancy.

First is the episodic context in which object individuation was investigated. In our paradigm, items could only be individuated using temporal cues, whereas participants in Xu and colleagues' studies could only rely on the items' spatial locations (see, Jeong & Xu, 2013; Xu, 2009; Xu & Chun, 2006; Xu & Chun, 2007). It is unknown how the neural mechanisms associated with object individuation processes differ between the spatial and temporal domains, and the types of paradigms used in these studies and the present study are too dissimilar to make any strong conclusions regarding how these two operations might be related. Further research using a single paradigm that can manipulate spatial and temporal individuation processes will be useful in informing us about the nature of these two processes in the brain. Second, Xu and colleagues examined a different

aspect of object individuation from the present study. Here we looked at the brain areas that support the process of individuation during perception, whereas Xu and colleagues' investigations focused on how individuated representations are consolidated, stored and retrieved in visual short-term memory. An interesting possibility could be that different groups of brain areas are recruited when individuated representations are constructed during perception and later stored in memory.

Could the neural operation associated with temporal individuation simply reflect other forms of repetition processing in the brain? Repetition suppression, for instance, is a phenomenon wherein the presentation of a repeated stimulus leads to a reduction in neural activity (Desimone, 1996; Grill-Spector, Henson, & Martin, 2006; Henson & Rugg, 2003; MacKay & Miller, 1994). Like the distributed signals that emerged in response to the differential demands placed on temporal individuation, repetition suppression has also been detected extensively throughout the brain (Gotts, Chow, & Martin, 2012). Our findings are unlikely to reflect repetition suppression for two key reasons, one reflecting methodology and the other a control analysis. First, the differential patterns of activity we observed for successfully individuating repeated and non-repeated stimuli were present after gross differences in mean BOLD amplitude were removed from each condition. Thus, the activity patterns that emerged for temporal individuation specifically reflect differences in spatial patterns of activity, not gross amplitude. Second, we were unable to decode purely stimulus-related changes in activity patterns associated with repeated and non-repeated stimuli (Hits and Misses versus Correct Rejections and False Alarms) in any ROI. Rather, the regions that could discriminate between Hits and Correct Rejections appear to be sensitive to the conditions under which the correct perceptual representation is successfully registered for a given stimulus. Our findings can therefore be distinguished from repetition suppression effects in the brain.

The present study also provides novel behavioural and fMRI evidence regarding the locus of RB. Although RB has been demonstrated for a variety of simple and complex stimuli (see, for a review, Coltheart, 2010), our behavioural findings extend the generality of RB by providing the first evidence that this deficit can occur for the perception of scenes. In addition, our univariate fMRI results provide new insights into the ongoing debate over whether RB reflects an early (Kanwisher, 1987; Luo & Caramazza, 1996) or late (Fagot & Pashler, 1995; Whittlesea & Masson, 2005) processing locus. Although the limited electrophysiological investigations into RB suggest that this deficit arises between 220-350 ms after the repeated stimulus appears (Koivisto & Revonsuo, 2008; Schendan, Kanwisher, & Kutas, 1997), the paradigms used in these studies do not exclusively tap the

capacity limits of individuation. To our knowledge, this study reflects the first neuroimaging work conducted using RB, where we found that the gross amplitude of BOLD activity in a higher-level premotor area – which has been previously implicated in processes such as top-down attention and response selection (e.g., Marois et al., 2006; Schumacher, Elston, & D'Esposito, 2003) – was influenced by whether participants successfully detected two repeated stimuli or not. Contrary to the prominent models of RB, this result suggests that this deficit has neither a purely perceptual or memory retrieval locus, but reflects a mid-level top-down attentional bottleneck in conscious awareness (see also, Chun, 1997).

The direction of amplitude differences for the capacity limits of temporal individuation might appear counter to what one would predict, as activity in the left hemisphere premotor cortex increased when a repetition was missed, compared with when it was correctly detected. Similar findings were noted in the AB literature, however, such that activity in two occipito-temporal regions were enhanced when two different letters were missed, relative to when they were detected (Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005). As RB is hypothesized to reflect an inability to bind an individuated token to a repeated type (Kanwisher, 1987; Park & Kanwisher, 1994), the enhanced activity associated with Miss trials could reflect maintenance of the second target's type representation as the visual system attempts (but is unable) to register the source of this representation. Similar to Kanwisher's original type-token account (Kanwisher, 1987; Park & Kanwisher, 1994), this interpretation suggests that the increased activation that emerged for Miss trials, relative to Hit trials, reflects changes in processing of the second target rather than the first.

The present findings also add to the existing literature on the relationship between RB and other capacity-limited processes such as the AB. Behavioural comparisons between these two phenomena have found similar results to our Lag RB experiment, in that they suggest that the AB and RB reflect distinct processing limitations (Chun, 1997; Dux & Marois, 2007). This apparent dissociation is further supported by the present fMRI findings, as we found different regions were implicated in RB relative to the AB, which has been associated with activity in parts of the lateral frontal, posterior parietal and occipito-temporal cortices (Kranczioch et al., 2005; Marcantoni, Lepage, Beaudoin, Bourgouin, & Richer, 2003; Marois et al., 2004). Although we are limited in making strong conclusions about the possible neural dissociation between the AB and RB, given that these investigations differed in paradigm and task, these findings do suggest that these two phenomena might be dissociable neurally as well as behaviourally. Our findings point

towards the possibility of exploring the dissociation or overlap in the brain between different bottlenecks in conscious awareness.

We have provided the first evidence for an extensive set of brain regions that support the process of temporal individuation in perception, as well as the neural consequences associated with the processing limitations that lead to the RB deficit. We found that varying the demands placed on temporal individuation produced distributed changes in the patterns of activity across the brain, suggesting that such processes operate within a widespread neuronal workspace and involve multiple sources of information (e.g., stimulus, decisional, response). In contrast, when the capacity limit of individuation is reached, there are focal increases in the gross amplitude of BOLD activity, possibly reflecting changes in the allocation of attentional resources to processing the second repeated target. These findings highlight apparent differences in the neural coding of two distinct processes associated with temporal individuation; namely, the demands under which individuated representations are generated and the capacity limits that bottleneck the binding of these individuated tokens to an identity representation for conscious report.

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CHAPTER 3: DISTRIBUTED AND OVERLAPPING NEURAL SUBSTRATES FOR OBJECT INDIVIDUATION AND IDENTIFICATION IN VISUAL SHORT-TERM MEMORY

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Abstract

Object individuation and identification are two key processes involved in representing visual information in short-term memory (VSTM). Individuation involves the use of spatial and temporal cues to register an object as a distinct perceptual event relative to other stimuli, whereas object identification involves extraction of featural and related conceptual properties of a stimulus. Together, individuation and identification provide the 'what', 'where' and 'when' of visual perception. In the current study, we asked whether individuation and identification processes are underpinned by distinct neural substrates, and to what extent brain regions that reflect these two operations are consistent across encoding, maintenance and retrieval stages of VSTM. We used functional magnetic resonance imaging to identify brain regions that represent the number of objects (individuation) and/or object features (identification) in an array. Using univariate and multivariate analyses, we found substantial overlap between these two operations in the brain. Moreover, we show that regions supporting individuation and identification vary across distinct stages of information processing. Our findings challenge influential models of multiple object encoding in VSTM which argue that individuation and identification are underpinned by a limited set of non-overlapping brain regions.

Many everyday activities, like searching for a stapler on a cluttered desk, rely on our ability to simultaneously isolate and identify multiple visual objects. To complete such a task, an observer must use spatial and temporal information to register each object as distinct (*object individuation*), and bind its features into a coherent form (*object identification*; Chun, 1997; Kahneman, Treisman, & Gibbs, 1992; Pylyshyn, 1989; Xu & Chun, 2009). It is currently unclear how these processes are represented in the brain. In their neural object file theory, Xu and Chun (2009) predict that the inferior intra-parietal sulcus (iIPS) plays a key role in object individuation, whereas the superior intra-parietal sulcus (sIPS) and lateral occipital complex (LOC) are involved in object identification (Jeong & Xu, 2013; Xu, 2007, 2008, 2009; Xu & Chun, 2007). Here we test Xu and colleagues' prediction of a strict functional dissociation between the contributions of these and other regions to object individuation and object identification.

In a pioneering study, Xu (2009) provided evidence for a dissociation between object individuation and identification within a single experiment. While undergoing functional magnetic resonance (fMRI) imaging, participants were briefly presented with a sample display consisting of one object, four identical objects or four different objects (see Figure 1). After a short delay, a single test item appeared centrally, and participants' task was to indicate whether the test identity matched one of the sample identities. Xu observed reduced blood oxygen level dependent (BOLD) activity in the iIPS for one-object displays, relative to both four-identical object and four-different object displays, which did not differ from each other. Conversely, the sIPS and LOC responded similarly for one-object and four-identical object displays, but both had reduced BOLD activity relative to four-different object displays. Consistent with the neural object file theory (Xu & Chun, 2009), these findings demonstrated that iIPS is sensitive to the number of objects in a display requiring individuation, whereas the sIPS and LOC respond to the number of distinct object identities requiring identification.

A potential shortcoming of Xu's (2009) study, and related empirical work (Jeong & Xu, 2013; e.g., Xu, 2007; Xu, 2008; Xu & Chun, 2007) upon which the neural object file theory is based, is that brain activity was analysed within occipital and parietal regions only, thus potentially missing contributions from other brain regions. Further, these studies employed univariate analyses of the fMRI data, which are less sensitive to small changes in patterns of BOLD response that can emerge when activity is analysed across groups of voxels (Haynes & Rees, 2005; Kamitani & Tong, 2005). Our recent work using multi-voxel pattern analysis (MVPA) suggests that temporal individuation – registering objects as distinct perceptual events based on when they appear in *time* – recruits a broad set of

frontal, parietal and occipital regions (Naughtin, Tamber-Rosenau, & Dux, 2013). Based on this work, we predicted that such widespread networks of brain activity might also emerge from MVPA analyses of fMRI data obtained for displays in which objects must be individuated and identified in the *spatial* domain.

Previous work on the neural object file theory has been also limited to paradigms with short retention intervals (Xu, 2009), meaning that these studies have not been able to examine individuation and identification during distinct visual short-term memory (VSTM) stages. It is important to consider the role of different processing stages, given VSTM has been hypothesised to involve encoding, maintenance and retrieval operations (e.g., Cohen et al., 1997; Courtney, Ungerleider, Keil, & Haxby, 1997). Although Jeong and Xu (2013; also see, Xu and Chun, 2006) did use a long-delay VSTM paradigm and suggested that the iIPS, sIPS and LOC are involved in individuation and identification processes during the encoding phase and beyond, their contrasts differed in both the number of objects presented, and the number object identities. Thus, they could not unambiguously compare individuation and identification processes.

Here we adopted a similar logic and approach to that used by Xu (2009), but with several important modifications, to test whether object individuation and identification can be dissociated in the brain (as suggested in the neural object file theory; Xu, 2009; Xu & Chun, 2009). We analysed activity across a broad set of brain regions using both univariate and MVPA approaches, and compared the role of each region across encoding, maintenance and retrieval stages of VSTM. In addition, unlike Xu's (2009) paradigm, our task required participants to remember both the identity *and* spatial location of all the objects in the display; this task ensured that both identification and individuation operations were engaged. By using both analytic approaches, we could first attempt to replicate the original univariate results from Xu (2009) under different task conditions, and also determine whether other brain regions show evidence of object identification or individuation using the more sensitive MVPA approach.

Materials and Methods

Participants

We recruited 21 volunteers to participate in the experiment (12 females, mean age = 25.7 years, *SD* = 3.4 years). Data from one participant were excluded due to excessive head motion, and from another due to a technical error that meant behavioural responses were not recorded. A post-hoc power analysis confirmed that a minimum sample size of 10

was sufficient to have an 80% chance of detecting similar effects (Cohen's *f*s > 1.13) to those reported by Xu (2009). Participants had normal or corrected-to-normal vision, gave informed consent, and were financially reimbursed for their time ($15/hour). The University of Queensland ethics committee approved the experimental protocol.

Design and Stimuli

Stimuli consisted of eight distinct shapes derived from Xu and Chun (2006). Each shape was presented in black on a light grey background (3.1º x 3.1º of visual angle). Stimuli could appear in one of eight dark grey placeholders (3.4º x 3.4º) arranged in a circular array, with each placeholder presented 5.3º from fixation. Placeholders were included to prevent grouping between closely presented objects (see Figure 1; Xu, 2009). The experiment was programmed in MATLAB using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

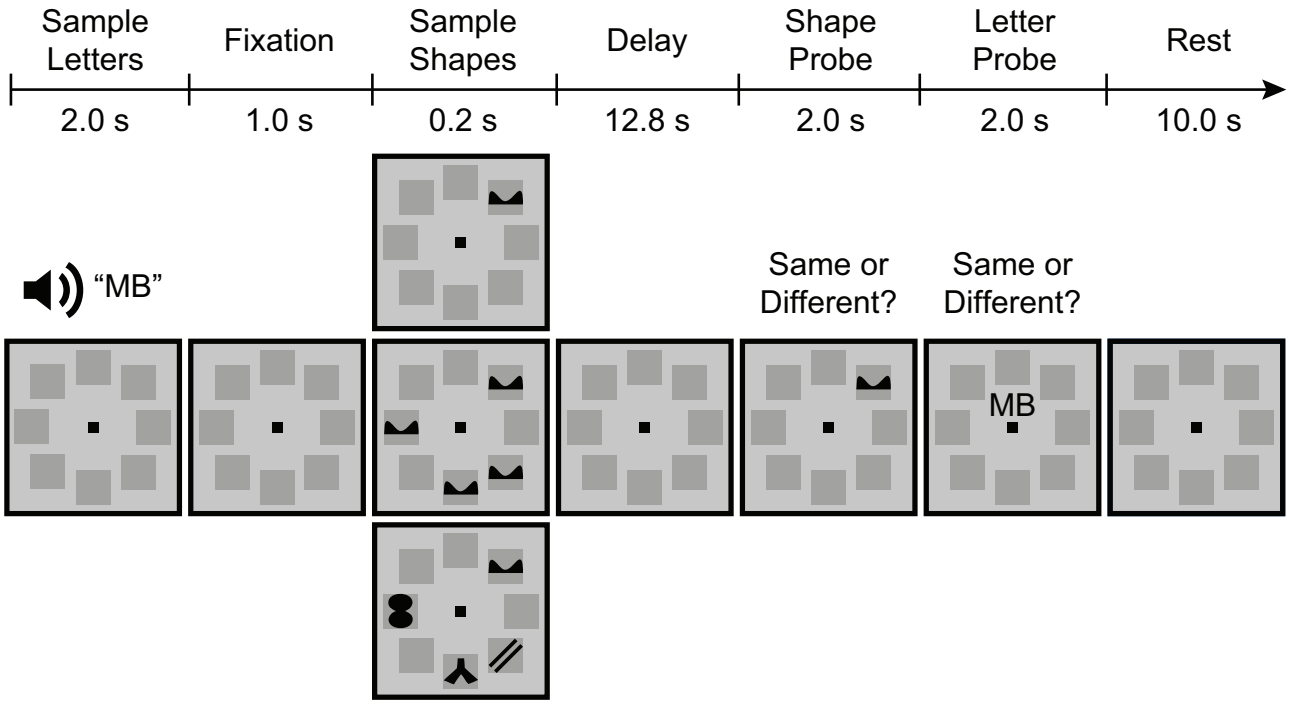

Figure 1. A schematic representation of the short-term memory paradigm.
Each trial began with the auditory presentation of two letters, followed by a sample display consisting of one object, four identical objects or four different objects. After an extended delay, observers identified whether a single test shape was the same as, or different from, one of the sample shapes, both in terms of its identity and location. The same judgement was also made for two subsequent test letters. The secondary auditory memory task was included to prevent participants from using verbal rehearsal strategies to remember the

shape stimuli. Stimuli were reproduced from Xu and Chun (2006) with permission from Nature Publishing Group.

Procedure

We used a STM paradigm, based on that of Xu (2009), to identify brain areas that selectively code for the number of objects (individuation) and/or number of object features (identification; see Figure 1). This paradigm had two components: A primary VSTM task and a secondary verbal memory task. Each trial began with the auditory presentation of two letters via headphones and participants were asked to rehearse these letters throughout the trial. The verbal memory task was included to prevent participants from using verbal rehearsal strategies for the visual stimuli (Todd & Marois, 2004). After a brief inter-stimulus interval, a sample display consisting of one object, four identical objects or four different objects was presented for 200 ms. Participants were instructed to remember the locations and identities of the sample objects during a subsequent 12.8 s retention interval. We used a slightly longer retention interval than is typically employed in slow event-related VSTM paradigms (e.g., see Emrich, Riggall, LaRocque, & Postle, 2013; Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009) to ensure that we could clearly distinguish between each stage of VSTM.

A single test shape appeared in one of the placeholders after the retention interval. The participants' task was to identify whether this test shape matched or mismatched one of the previously presented sample shapes, both in terms of its identity *and* location. It is important to note that a correct response on this task required that participants successfully individuate and identify each of the sample items, rather than merely their identity (cf. Jeong & Xu, 2013; Xu, 2009, 2010; Xu & Chun, 2007). Thus, even though the four identical-object displays only contained a single identity, participants still had to individuate where each object appeared to produce a correct response. Two test letters were then presented, and participants made the same match/mismatch response for these letters, relative to the two sample letters presented at the beginning of the trial. Only response accuracy was emphasised, but participants had a fixed interval of 2 s in which to make each of their responses. The test shape and letter matched or mismatched one of the sample items an equal number of times.

Each trial was followed by a 12 s fixation period. This experimental design allowed us to isolate sources of BOLD activity previously associated with encoding, maintenance and retrieval of the visual information (e.g., see Emrich et al., 2013; Harrison & Tong, 2009; Serences et al., 2009). We chose to use these labels for the different time periods

because previous studies have used them to describe the distinct phases of activity observed across long retention intervals. A more theoretically neutral approach might be to label the stages as 'early,' 'middle' and 'late', but we chose to adopt the former set of labels to be consistent with prior VSTM studies (e.g., Todd & Marois, 2004; Xu & Chun, 2006).

Participants completed 6 practice trials outside the scanner, followed by 8 scanning runs of 12 test trials. We only provided feedback for incorrect responses on practice trials, in which the central fixation square briefly turned red. Each run contained an equal number of trials per trial type. Trial types were presented in a randomised order and the selection of stimuli and their locations were randomised across trials. Preliminary pilot testing ensured that participants could complete the task with a high level of accuracy (>80%). We made sure participants could perform this task well, as only correct trials were included in the fMRI analyses.

fMRI Acquisition

We acquired anatomical and functional images using a 3T Siemens Trio MRI scanner (Erlangen, Germany) and a 12-channel head coil. Participants lay supine in the scanner and viewed the visual display via a rear-projection mirror. Functional T2*-weighted images were acquired parallel to the AC-PC plane using a GRE EPI sequence (TR = 2 s, TE = 25 ms, flip angle = 90º, FOV = 192 x 192, matrix = 64 x 64, in-plane resolution = 3 x 3 mm). Each volume consisted of 33 slices with a thickness of 3 mm and a 0.3 mm inter-slice gap. In the middle of the session, we collected a T1-weighted anatomical image using a MPRAGE sequence (TR = 1.9 s, TE = 2.32 ms, flip angle = 9º, FOV = 192 x 230 x 256, resolution = 1 mm^3). We synchronised the stimulus presentation with the acquisition of functional volumes. Each run consisted of 184 volumes, including an 8 s dummy fixation block presented at the start of the run.

fMRI Analyses

We conducted pre-processing, univariate analyses and MVPA with Brain Voyager QX 2.4 (Brain Innovation, Maastricht, Netherlands) and custom MATLAB code. We used both univariate and MVPA techniques to test for overall differences in BOLD amplitude and changes in the spatial patterns of activity across groups of voxels for each condition, respectively. There were two key comparisons of interest: First, to identify regions that reflect object individuation, we compared activity between displays containing one object and those containing four identical objects. Regions associated with this process should

be sensitive to the episodic properties of objects (i.e., the number of objects in the display), but not to object identity (since this remained constant across the two display types). Second, to isolate regions that support object identification, we compared activity for displays containing four identical objects with those containing four different objects. If a given brain region specifically contributes to object identification, it should show a difference in activity in response to the number of distinct identities present, rather than to the number of objects per se. These were the same comparisons previously used by Xu (2009).

Pre-processing. Data pre-processing steps consisted of 3D motion correction (with all functional images aligned to the first image), slice-scan time correction, high-pass temporal filtering (3 cycles per run) and Talairach space transformation (Talairach & Tourmoux, 1988). We did not apply spatial smoothing to the data to preserve fine-grained changes in activity for MVPA (as described in detail below).

Regions of interest. All ROIs were defined anatomically using mean Talairach coordinates from other relevant published studies. We used coordinates from Xu and Chun (2006) to define the iIPS, sIPS and LOC, which have previously been implicated in object individuation and identification (e.g., Xu, 2009; Xu & Chun, 2009). To explore the role of other regions, we also isolated a set of frontal, parietal and occipital regions involved in higher-level resource-limited processes such as response selection, decision making and encoding (Dux, Ivanoff, Asplund, & Marois, 2006; Dux et al., 2009; Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Naughtin et al., 2013; Szametitat, Schugbert, Muller, & von Cramon, 2002; Tombu et al., 2011). Talairach coordinates for these regions were derived from our previous published studies (Dux et al., 2009; Naughtin et al., 2013). Since the sIPS and superior parietal lobule (SPL) ROIs overlapped in the majority of participants, we averaged the results across these two regions (referred to as sIPS/SPL).

ROIs were defined by an 11 mm^3 cube for the univariate analyses (we used the same number of voxels in each ROI as Xu, 2009) and a 15 mm^3 or 21 mm^3 cube for MVPA. In both cases, the ROI cube was centered on the mean Talairach coordinates. We defined each ROI using a larger number of voxels for MVPA, compared with the univariate analyses, as it is conventional to use larger ROIs in the former to provide increased variability across voxels (e.g., Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011; Harrison & Tong, 2009; Kamitani & Tong, 2005; Oosterhof, Tipper, & Downing, 2012). As the sensitivity of MVPA depends upon the number of voxels included in the analysis, we used two different ROI sizes for MVPA – rather than choosing an arbitrary ROI size – to ensure the results were reliable, regardless of the number of voxels included in the

classification analysis (Carp, Park, Polk, & Park, 2011; Naughtin et al., 2013; Spiridon & Kanwisher, 2002). For simplicity, we report the MVPA results from the 21 mm^3 ROIs that were significant across both ROI sizes. In addition to our main experimental ROIs, we also used the left and right primary auditory cortices as control regions (see also, Naughtin et al., 2013). As these areas primarily respond to auditory information rather than visual information (e.g., pitch; Hyde, Peretz, & Zatorre, 2008), they should not show any evidence of individuation or identification. The auditory cortex control regions were defined in the same way as the other ROIs, with the ROI cube centered on the superior portion of the temporal lobe (Rademacher et al., 2001).

Univariate analysis. The purpose of the univariate analysis was to identify gross changes in BOLD amplitude that have been hypothesized to reflect the processes of individuation or identification. We extracted timecourses for each display condition with percentage signal change at each time point calculated relative one volume prior to trial onset. This procedure was performed separately for each ROI and participant. To determine the peak amplitude for encoding, maintenance and retrieval, we collapsed timecourses across all display types, participants and ROIs, and selected the two volumes corresponding to the peak at each stage. The time windows for the encoding, maintenance and retrieval stages of VSTM were 4-8 s, 12-16 s and 18-22 s after sample display onset, respectively (similar to previous VSTM studies, Jeong & Xu, 2013; Todd & Marois, 2004; Xu & Chun, 2006).

Multivariate analyses. MVPA was employed to assess for individuation- or identification-related changes in activity that may be present in the ensemble patterns of activity of each ROI (Haynes & Rees, 2006; Kamitani & Tong, 2005). This type of approach is more sensitive to small, reliable changes in activity that might not be detected in standard univariate analyses. We used custom MATLAB software and a linear support vector machine algorithm (Chang & Lin, 2011) for these analyses. We ran separate classification analyses for encoding, maintenance and retrieval stages for each ROI; data for each voxel were averaged across the respective time windows (4-8, 12-16 and 18-22 s after sample display onset). Prior to MVPA, these data samples were transformed into z-scores and mean-centered to remove any amplitude differences between conditions (Esterman, Chiu, Tamber-Rosenau, & Yantis, 2009; Tamber-Rosenau, Esterman, Chiu, & Yantis, 2011). To assess classification performance, we used the leave-one-out cross-validation procedure. On each loop, one run was reserved to test the classifier's generalisation performance and the remaining seven runs were used to train the classifier. We averaged classification performance for each ROI across all cross-validation loops and

compared this accuracy to chance performance (50%) using a one-sample *t*-test ($p < .05$, Bonferroni corrected for the number of ROIs and number of VSTM stages tested).

Results

Behavioural performance

Performance on the verbal memory task did not differ between the three display types (88.7-90.6% accuracy across all display types; $F < 1$), which is consistent with the idea that auditory and visual short-term memory systems operate independently of each other (Baddeley, 1992; Smith & Jonides, 1998). We used Cowan's *K* formula (Cowan, 2001) to estimate participants' VSTM capacity for each display type in the visual memory task. As shown in Figure 2, *K* estimates significantly differed across display types, $F(2, 36) = 75.21$, $p < .001$, $\eta_p^2 = 0.81$. Behavioural performance was close to ceiling for one object and four identical objects, but participants could only hold about two objects in memory for the four-different object displays.

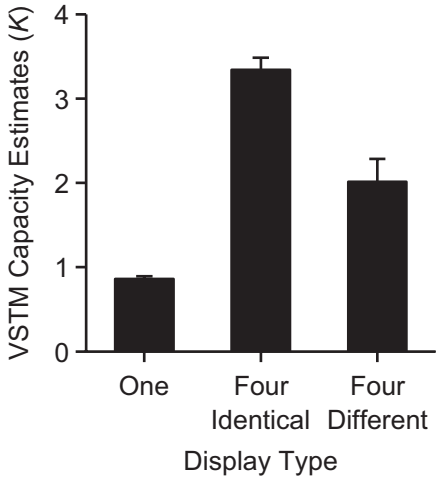

Figure 2. Behavioural estimates of visual short-term memory capacity as a function of the three display types.

These estimates were calculated using Cowan's (2001) *K* formula. Error bars denote one standard error of the mean. VSTM, visual short-term memory.

Univariate Analyses

We first tested for gross differences in BOLD amplitude associated with individuation and identification processes. For each comparison, we conducted a repeated-measures analysis of variance (ANOVA) with factors of display type (one object,

four identical objects, four different objects) and stage (encoding, maintenance, retrieval), separately for each ROI. A significant main effect of display type indicates that a given region is consistently modulated by one or both of the processes of interest (i.e., the number of objects – *individuation*; or the number of object features – *identification*) and a significant display type by stage interaction signals that activity associated with the process(es) of interest varies across different VSTM stages. Whenever the analysis for a given region yielded a significant interaction, we ran follow-up *t*-tests at each VSTM stage to identify the stage(s) at which that region was recruited for the process(es). We present results from the significant regions according to whether they were modulated by the number of objects, the number of object features, or both.

Individuation-related activity. Areas associated with object individuation either showed an overall amplitude difference between one-object versus four-identical object displays, or an interaction between these two display types and stage (see Figure 3). We found the left and right iIPS were showed a significant main effect of display type, *F*s(2, 36) > 4.44, *p*s < .024, η_p^2s > .20, and follow-up *t*-tests revealed that activity was significantly reduced for displays with one-object, compared with four-identical object displays, *t*s(18) > 2.95, *p*s < .009. The comparison between four identical objects and four different objects was not significant, *t*s(18) < 1.08, *p*s > .294. Consistent with previous work by Xu (2009), we found a profile in the univariate activity that suggests that the iIPS is recruited for object individuation and not object identification. Here we also show, for the first time, that the involvement of these regions in individuation is consistent across all three VSTM stages.

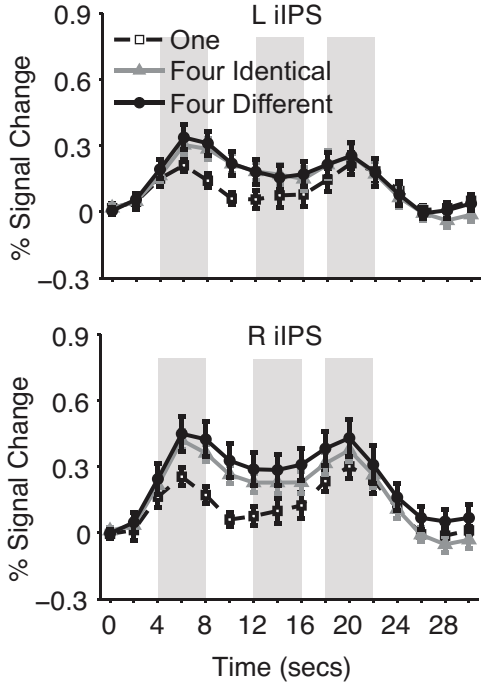

Figure 3. Blood oxygen level dependent timecourses during encoding, maintenance and retrieval stages for regions that were influenced by the number of objects in the display (reflecting object individuation).

These areas showed a significant difference between one-object and four-identical object displays at one or more visual short-term memory (VSTM) stages. Separate lines denote display types and the shaded grey areas reflect the time window used for each stage of VSTM. Error bars denote one standard error of the mean. Region abbreviations are: iIPS, inferior intra-parietal sulcus; L, left; R, right.

Identification-related activity. We identified areas that support object identification as those for which there were significant amplitude differences between four-identical object displays and four-different object displays, or an interaction between these two display types and stage (see Figure 4). The anterior cingulate cortex (ACC) and the right dorsolateral prefrontal cortex (DLPFC) showed a significant main effect of display type, *F*s(2, 36) > 3.62, *p*s < .040, η_p^2s > .17. Follow-up *t*-tests revealed that this effect was driven by an enhanced response for four different objects versus four identical objects, *t*s(18) > 2.40, *p*s < .027.

Five additional ROIs showed a significant display type x stage interaction, *F*s(4, 72) > 2.87, *p*s < .047, η_p^2s > .14 (four of which also showed a significant effect of display type, *F*s(2, 36) > 5.14, *p*s < .011, η_p^2s > .22): superior medial frontal cortex (SMFC), right premotor cortex (PMC), bilateral insula and left inferior frontal junction (IFJ). All these

regions showed a significant difference in activity between four identical and four different objects for the encoding and maintenance time windows, *t*s(18) > 2.06, *p*s < .054, and the right insula also showed a significant difference at retrieval, *t*(18) = 3.17, *p* = .005. Unlike the individuation results, in a task where both identity and location information had to be processed, we failed to observe Xu's (2009) finding that object identification is restricted to the sIPS and LOC. Instead, we found a different set of brain regions was associated with this process, and these regions were active during the encoding and maintenance time windows.

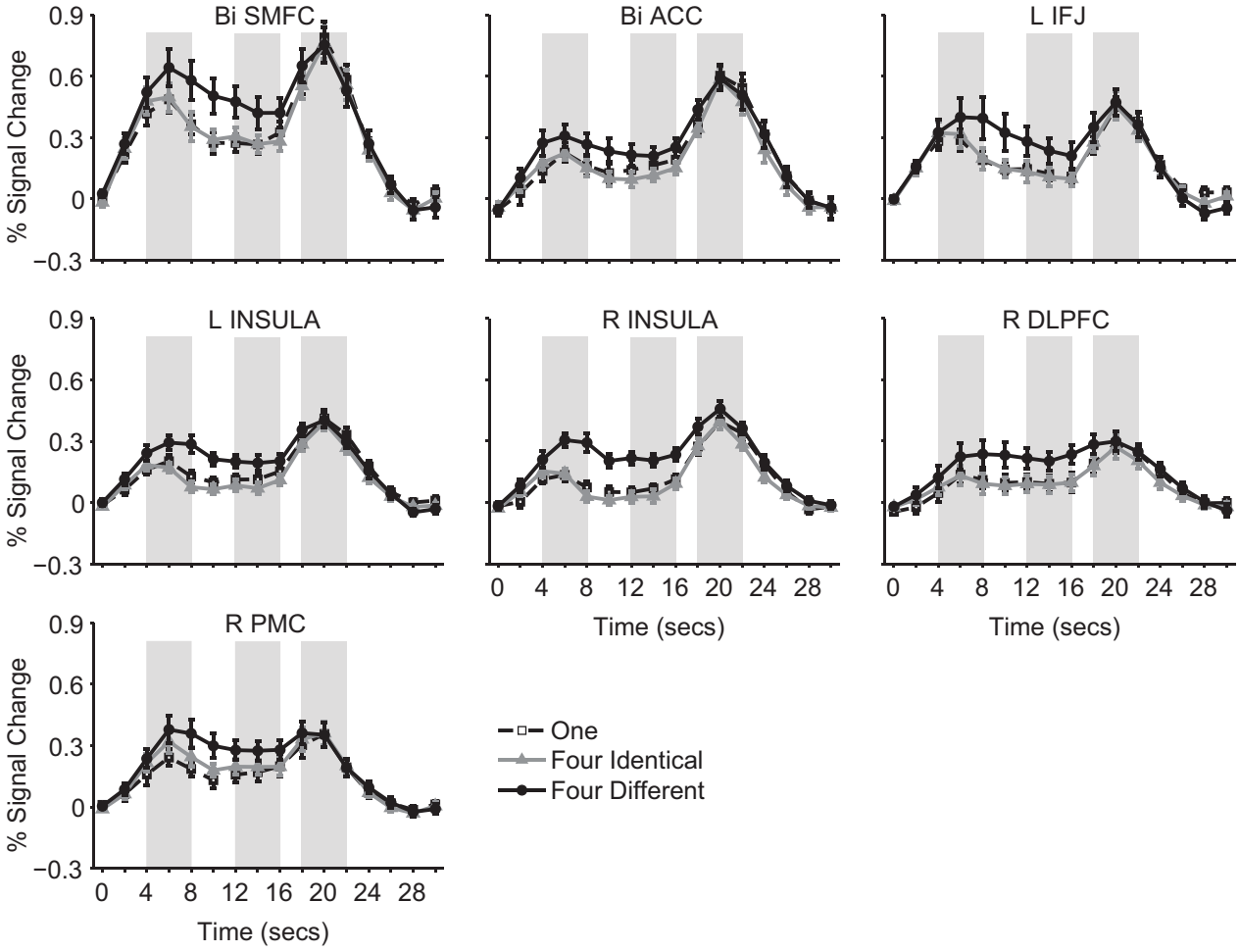

Figure 4. Blood oxygen level dependent timecourses during encoding, maintenance and retrieval periods for regions that were influenced by the number of object features in the display (reflecting object identification).

These regions showed a significant difference between displays containing four identical objects and those with four different objects at one or more visual short-term memory (VSTM) stages. Separate lines denote display types and the shaded grey areas reflect the time window used for each stage of VSTM. Error bars denote one standard error of the

mean. Region abbreviations are: SMFC, superior medial frontal cortex; ACC, anterior cingulate cortex; IFJ, inferior frontal junction; DLPFC, dorsolateral prefrontal cortex; PMC, premotor cortex; Bi, bilateral; L, left; R, right.

Individuation- and identification-related activity. In addition to those regions that were modulated either by the number of objects (individuation) or object features (identification), we also found some regions that showed evidence of *both* processes: Left PMC, right IFJ and bilateral sIPS/SPL (see Figure 5). These four regions showed a significant interaction between display type and stage, *F*s(4, 72) > 4.09, *p*s < .005, η_p^2s > .19. Follow-up *t*-tests revealed that all regions showed a difference between one object and four identical objects at encoding, *t*s(18) > 2.01, *p*s < .059. A significant difference between one-object and four-identical objects displays was also observed during maintenance in the bilateral sIPS/SPL regions, *t*s(18) > 2.15, *p*s < .045, and in the right hemisphere sIPS/SPL during retrieval, *t*(18) = 2.66, *p* = .016. For the identification comparison, activity was significantly reduced for four-identical object displays versus four-different object displays for the left PMC, right IFJ and bilateral sIPS/SPL during encoding and maintenance, *t*s(18) > 2.11, *p*s < .049. Contrary to what Xu and Chun originally proposed (Xu, 2009; Xu & Chun, 2009), these findings suggest that individuation and identification cannot be completely dissociated in the brain under conditions where identity and location must be analysed, as our univariate results revealed a subset of brain areas that are involved in *both* operations.

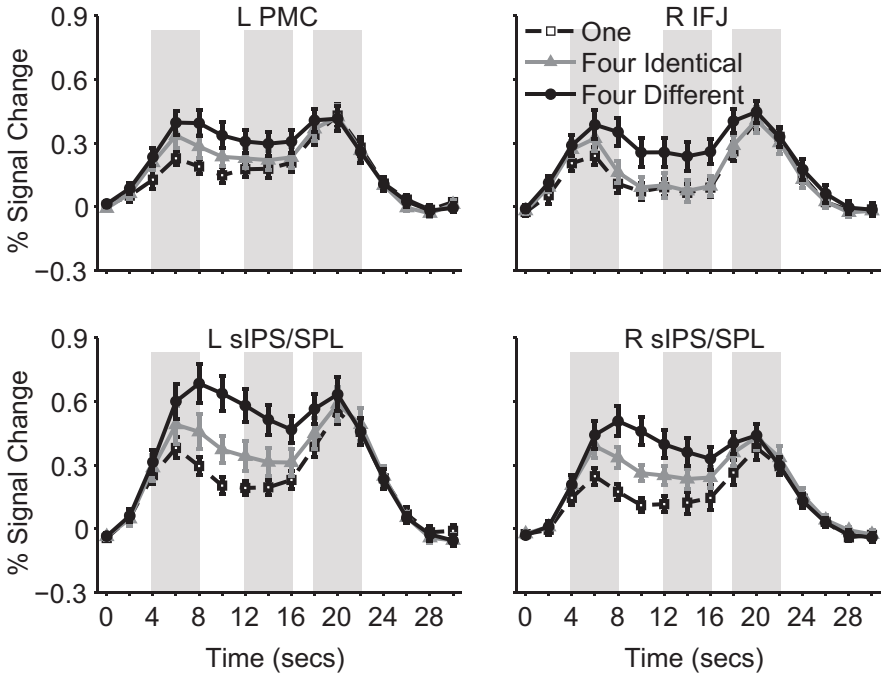

Figure 5. Blood oxygen level dependent timecourses during encoding, maintenance and retrieval periods for regions that were influenced by both the number of objects (object individuation) and number of object features (object identification).
These regions showed significant differences between both comparisons of interest at one or more visual short-term memory (VSTM) stages. Separate lines denote display types, and the shaded grey areas reflect the time window used for each stage of VSTM. Error bars denote one standard error of the mean. Region abbreviations are: PMC, premotor cortex; IFJ, inferior frontal junction; sIPS/SPL, superior intra-parietal sulcus/superior parietal lobule; L, left; R, right.

Multivariate Analyses

Similar to the univariate analyses, we conducted MVPA on data corresponding to encoding, maintenance and retrieval stages of VSTM. In separate analyses, we trained a classifier to discriminate between the same two key comparisons used in the univariate analyses: One object versus four identical objects for individuation, and four identical objects versus four different objects for identification. Classification performance for each ROI was compared to chance (50%) using a one-sample *t*-test and a significance threshold of $p < .05$, Bonferroni corrected for the 18 regions tested (i.e., 16 main regions of interest plus 2 control regions) and the 3 VSTM stages (critical $p = .0009$).

Compared with the univariate analyses, the MVPA approach revealed a more extensive neural overlap between individuation and identification processes (see Figure

6). Six regions displayed evidence of either individuation or identification processes. Specifically, right IFJ, bilateral insula and left LOC showed significant decoding for the number of objects, *t*s(18) > 4.47, *p*s < .016 (corrected), whereas the right DLPFC showed significant decoding for the number of object features, *t*(18) = 4.78, *p* = .008 (corrected). For nine of the sixteen regions – the left IFJ, left sIPS/SPL, left LOC, ACC, SMFC, and bilaterally in the PMC and iIPS – classifiers could decode activity between the 'number of objects' comparison (one object versus four identical objects) and the 'number of object features' comparison (four identical versus four different objects) in one or more VSTM stages, *t*s(18) > 4.06, *p*s < .040 (corrected). This finding suggests that these regions represent individuation *and* identification processes, rather than one distinct process. In addition, while activity associated with the number of objects or object features could be decoded across all VSTM stages in some regions (e.g., bilateral sIPS/SPL, left PMC, right LOC), other brain areas were recruited during specific stages (e.g., within the left IFJ, the number of object features presented could be decoded during encoding and maintenance, but the number of objects per se could be decoded at retrieval only).

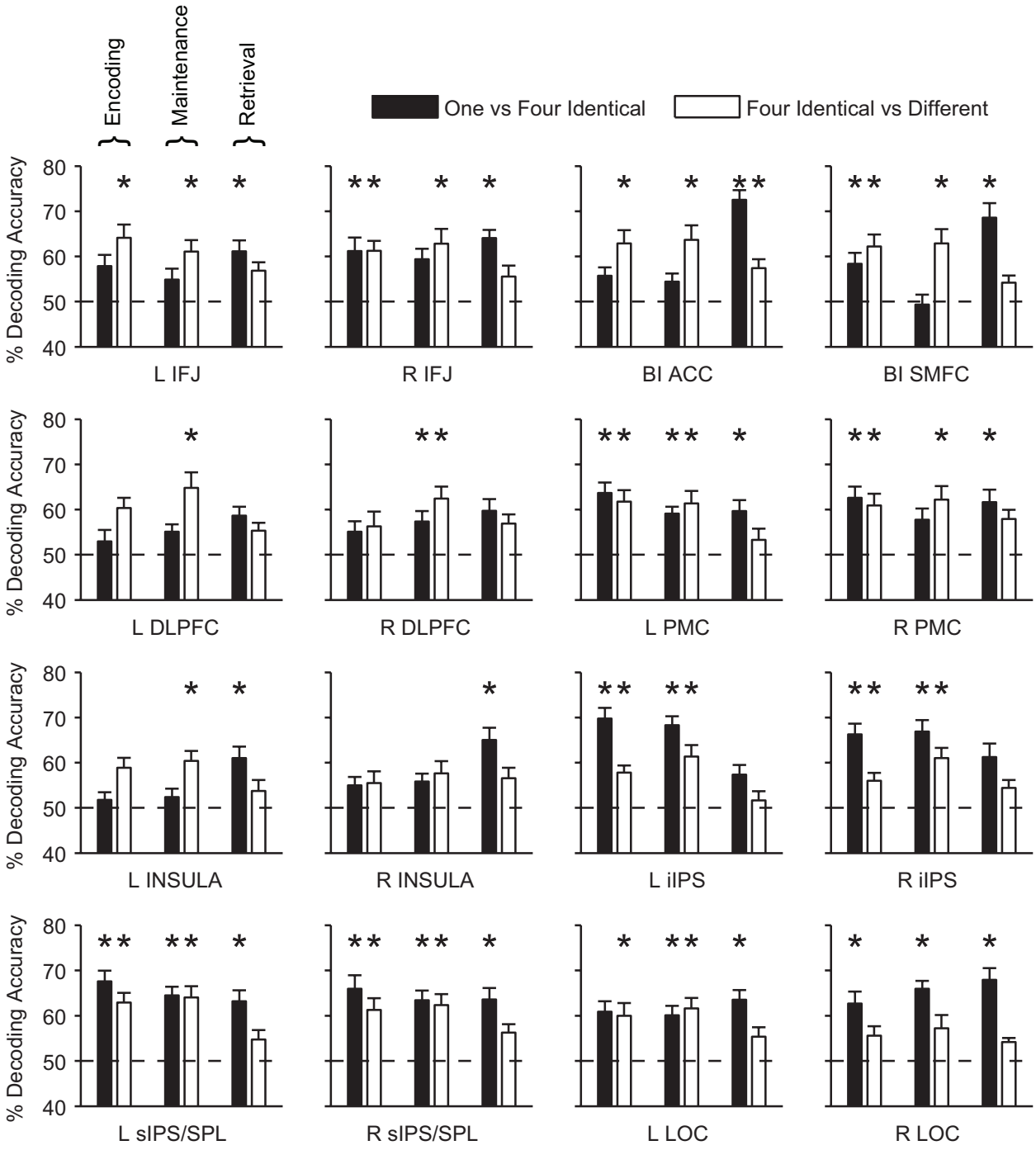

Figure 6. Mean classification performance during encoding, maintenance and retrieval periods across all key regions of interest.

Classifiers were trained to discriminate between the two key comparisons: One object versus four identical objects ('number of objects' comparison; *object individuation*), and four identical objects versus four different objects ('number of object features' comparison; *object identification*). Results from each region are displayed on separate plots. Asterisks denote classification performance that is significantly greater than chance across both ROI sizes (Bonferroni-corrected for the number of regions and VSTM stages tested). Error bars

reflect standard error of the mean. Region abbreviations are: IFJ, inferior frontal junction; ACC, anterior cingulate cortex; SMFC, superior medial frontal cortex; DLPFC, dorsal lateral prefrontal cortex; PMC, premotor cortex; SPL, superior parietal lobule; sIPS/SPL, superior intra-parietal sulcus/superior parietal lobule; iIPS, inferior intra-parietal sulcus; LOC, lateral occipital complex; Bi, bilateral; L, left; R, right.

Taken together, these findings suggest an extensive interplay between object individuation and identification in the brain, and suggest that signals associated with these processes can be detected across a wide network of regions at each stage of VSTM (see also, Naughtin et al., 2013). These findings are inconsistent with the neural object file theory put forward by Xu and Chun (2009), which predicts that individuation and identification are subserved by a limited set of non-overlapping brain regions. Rather, we show that activity is modulated in a distributed set of common regions when observers are required to identify and individuate a set of items in a display (novel conditions that are not accounted for in the current conceptualisation of the neural object file theory).

One caveat to these conclusions is that the differences we observed for individuation and identification could instead reflect some general, unspecified effect of task difficulty. As we elaborate on in the General Discussion, such task difficulty effects are a potential issue for any study where there are behavioural differences between conditions (including the previous work by Xu and colleagues). It is therefore challenging to operationalize general, unspecified effects of task difficulty as a measure that is independent of the manipulated factors. Nevertheless, as MVPA has the potential to exacerbate such difficulty effects (e.g., see Todd, Nystrom, & Cohen, 2013), we addressed this issue by balancing reaction times across our two key comparisons of interest. Prior to conducting the MVPAs, we equated reaction times between the ‘number of objects’ and ‘number of object features’ comparisons by removing the slowest trials from the condition with the longest average reaction time and the fastest trials from the condition with the shortest average reaction time, until there was no significant reaction time difference between the conditions, ts(14) < 1.56, ps > .141. Data from four participants were removed from these analyses, as we could not balance their reaction times between conditions for one or both comparisons (leaving the sample at n = 15).

Despite the substantial reduction in power due to fewer trials and subjects included in this analysis, we found 32 of our original 43 significant decoding effects held once reaction time was equated (see Table 1). The number of objects and/or object features could no longer be discriminated in the maintenance or retrieval periods for the left IFJ,

right DLPFC, bilateral PMC, left insula and right sIPS/SPL (*p*s > .05, corrected, across one or both ROI sizes). For the encoding period, the number of objects in the right LOC and the number of object features in the left PMC could not be reliably discriminated (*p*s > .05, corrected, across one or both ROI sizes). It is possible that those effects that were no longer reliable reaction time balanced analysis might have reflected some general effect of task difficulty, rather than the processes of interest. An alternative explanation is that this control analysis simply had less power than the main analysis to detect these effects, due to the reduction in trial numbers and subjects. Although these reaction time controlled results raise a degree of doubt about the role played by some of our ROIs in individuation and identification, the overall results were largely robust to this balancing procedure. Collectively, our findings demonstrate that individuation and identification processes can be detected in overlapping substrates that are distributed across the brain.

Table 1. Mean classification performance during encoding, maintenance and retrieval periods for the main decoding analysis (where reaction time was not equated) and the task difficulty control analysis (where reaction time was equated). Standard deviations are denoted in the parentheses. Decoding accuracies for each region are displayed separately for the 'number of objects' comparison (one object versus four identical objects, 1 vs. 4I) and the 'number of object features' comparison (four identical objects versus four different objects, 4I vs. 4D). All statistical results are Bonferroni-corrected for the number of regions and visual short-term memory stages tested. $^{*}p < .050$, $^{\#}p < .082$ (marginally significant). Region abbreviations are the same as Figure 6. RTs, reaction times; VSTM, visual short-term memory.

	VSTM: Encoding		**VSTM: Maintenance**		**VSTM: Retrieval**	
Region of Interest	**Unequal RTs**	**Equal RTs**	**Unequal RTs**	**Equal RTs**	**Unequal RTs**	**Equal RTs**
IFJ (L)						
1 vs. 4I	57.8 (11)	56.1 (11)	54.9 (10)	56.1 (12)	61.1 (10)*	59.5 (9)
4I vs. 4D	64.1 (12)*	68.8 (15)*	61.1 (11)*	62.9 (12)	56.8 (8)	61.5 (12)
IFJ (R)						
1 vs. 4I	61.2 (13)	60.3 (15)	59.4 (10)	59.5 (12)	64.0 (8)*	63.2 (9)*
4I vs. 4D	61.2 (9)	62.1 (12)	62.8 (14)	63.8 (15)	55.6 (10)	64.7 (15)$^{\#}$

ACC (Bi)						
1 vs. 4I	55.7 (8)	55.4 (10)	54.4 (8)	55.2 (10)	72.5 (9)*	73.3 (9)*
4I vs. 4D	62.9 (12)*	67.0 (15)*	63.6 (14)*	66.8 (15)*	57.4 (9)	73.1 (11)*
SMFC (Bi)						
1 vs. 4I	58.3 (10)	60.0 (12)	49.4 (9)	52.8 (11)	68.6 (14)*	69.2 (12)*
4I vs. 4D	62.2 (11)*	67.2 (9)*	62.9 (13)*	66.6 (13)*	54.2 (7)	67.6 (13)
DLPFC (L)						
1 vs. 4I	52.9 (11)	54.5 (11)	55.1 (7)	56.9 (11)	58.6 (8)	55.1 (8)
4I vs. 4D	60.3 (10)	62.6 (14)	64.8 (15)	64.9 (15)	55.3 (8)	60.3 (12)
DLPFC (R)						
1 vs. 4I	55.1 (10)	55.5 (11)	57.3 (10)	58.2 (11)	59.7 (11)	60.1 (12)
4I vs. 4D	56.3 (14)	60.3 (14)	62.4 (11)*	65.2 (13)	56.9 (9)	60.7 (10)*
PMC (L)						
1 vs. 4I	63.6 (10)*	66.1 (12)*	59.1 (6)*	61.4 (10)	59.7 (10)*	59.7 (11)
4I vs. 4D	61.7 (11)*	61.4 (11)	61.3 (12)*	62.5 (12)	53.3 (11)	62.3 (14)
PMC (R)						
1 vs. 4I	62.6 (11)*	63.7 (9)*	57.7 (11)	57.9 (13)	61.7 (12)*	58.5 (14)
4I vs. 4D	60.9 (11)*	64.8 (13)*	62.2 (13)*	64.0 (14)#	57.9 (9)	62.1 (11)
Insula (L)						
1 vs. 4I	51.8 (7)	52.3 (12)	52.4 (8)	54.3 (10)	61.0 (11)*	59.2 (10)
4I vs. 4D	58.9 (9)	61.7 (12)	60.4 (9)	63.8 (10)	53.7 (10)	59.5 (14)
Insula (R)						
1 vs. 4I	55.0 (8)	54.7 (9)	55.8 (7)	56.9 (10)	65.0 (11)*	63.9 (13)#
4I vs. 4D	55.5 (11)	60.3 (16)	57.6 (11)	62.8 (11)*	56.6 (10)	63.0 (12)*
iIPS (L)						
1 vs. 4I	69.8 (10)*	66.2 (12)*	68.3 (8)*	67.2 (9)*	57.3 (9)	57.4 (7)
4I vs. 4D	57.8 (7)*	67.2 (13)*	61.3 (11)*	65.3 (12)*	51.6 (9)	59.8 (14)
iIPS (R)						
1 vs. 4I	66.3 (10)*	65.1 (12)*	66.9 (11)*	69.7 (12)*	61.2 (13)	59.4 (13)
4I vs. 4D	56.0 (7)	65.3 (14)*	61.0 (10)*	66.9 (11)*	54.4 (7)	59.0 (12)

sIPS/SPL (L)						
1 vs. 4I	67.6 (10)*	67.4 (10)*	64.5 (8)*	63.7 (10)*	63.2 (10)*	61.8 (11)*
4I vs. 4D	62.9 (9)*	68.7 (11)*	64.0 (10)*	66.5 (12)*	54.8 (9)	67.0 (10)*
sIPS/SPL (R)						
1 vs. 4I	66.0 (13)*	66.7 (13)*	63.4 (9)*	65.1 (10)*	63.6 (11)*	62.7 (12)
4I vs. 4D	61.3 (11)	67.0 (14)*	62.3 (10)	66.6 (12)*	56.2 (8)	63.6 (11)*
LOC (L)						
1 vs. 4I	60.9 (10)	62.4 (10)*	60.1 (9)*	62.8 (8)*	63.5 (9)*	62.2 (11)*
4I vs. 4D	60.0 (12)	64.8 (14)	61.6 (10)*	67.6 (11)*	55.4 (9)	60.6 (13)
LOC (R)						
1 vs. 4I	62.7 (11)*	60.1 (12)	66.0 (7)*	66.7 (6)*	67.9 (11)*	67.5 (12)*
4I vs. 4D	55.6 (9)	61.2 (12)	57.2 (13)	58.0 (11)	54.2 (4)	68.8 (11)*

Control Analysis

We conducted the same MVPAs using data from two control regions (left and right auditory cortices) that should not be involved in visual individuation or identification. The purpose of this control analysis was to ensure that the decoding differences described above reflect the processes of interest – object individuation and identification – rather than any unanticipated artifact of our data, task design or analyses. As expected, classifiers could not reliably discriminate between the number of objects in the display (one object versus four identical objects) or the number of object features (four identical objects versus four different objects) in the left or right auditory cortices at any VSTM stage, *t*s(18) = 2.64, *p*s > .855 (corrected). These control results confirm that the observed differences between the display types within the experimental ROIs reflect processes specifically associated with individuating or identifying multiple objects.

General Discussion

The purpose of the current study was twofold: We wanted to test whether object individuation and identification are distinct processes in the brain, and whether the brain regions that support these operations vary across different processing stages of VSTM. Using the same logic and a similar experimental approach to that previously employed by Xu (2009), we compared changes in BOLD activity under conditions that differed in either the number of objects (one object versus four identical objects) or the number of object features (four identical objects versus four different objects). We used a slow event-related

protocol that allowed us to separate activity reflected by encoding, maintenance and retrieval VSTM stages. Across both univariate analyses and MVPA, we found evidence for both distinct and overlapping neural substrates for individuation and identification. The overlap between these two operations was most apparent in the MVPA results, where nine ROIs showed evidence of individuation and identification at a single or multiple VSTM stages. These results suggest that individuation and identification have distributed and overlapping neural substrates (see also, Naughtin et al., 2013), and these operations are not restricted to a few process-specific brain areas, as has previously been suggested (Xu, 2009; Xu & Chun, 2009).

The involvement of most brain regions in individuation and identification was variable across VSTM stages, particularly at retrieval. The timing of the auditory memory response, however, could account for the absence of individuation- or identification-related activity at the retrieval stage. In other words, activity associated with the auditory memory response could have obscured effects present in the visual memory response. By contrast, the observed modulations associated with differences in number of objects or object features in the display could not simply reflect an artifact of our data, task design or analysis, as these same comparisons yielded no significant decoding in two auditory control regions.

One could argue that data from our main analyses do not rule out the potential confound of general, unspecified task difficulty. In fact, such difficulty is also a possible issue for the prior studies by Xu and colleagues, and likely any other study in cognitive neuroscience where performance differs between conditions (e.g., the standard parametric manipulation). Similarly, it is equally problematic to interpret imaging findings when there is no behavioural difference between conditions. Here we find complementary differences in behaviour and the brain. In an attempt to rule out the potential confound of task difficulty, we equated reaction times between our two key comparisons, and the results were largely comparable to those from our main decoding analysis. We still found activity in a distributed set of brain regions that was specifically associated with individuation or identification, and seven of the original nine regions showed evidence of both processes (ACC, SMFC, right PMC, bilateral iIPS, left sIPS/SPL and left LOC). Thus, any non-specific effect of difficulty cannot account for the overlap between individuation and identification that we observe.

The large number of common brain regions associated with individuation and identification, either at the same stage or different stages of VSTM, contrasts with theoretical accounts and fMRI results put forward by Xu and colleagues (Jeong & Xu,

2013; Xu, 2009; Xu & Chun, 2006, 2007, 2009). For example, Xu (2009) used univariate analyses and found evidence for individuation tapping only the iIPS and identification only the sIPS and LOC. Within these three posterior regions, however, we found the greatest overlap between individuation and identification, particularly during encoding and maintenance VSTM stages. These discrepant findings resonate with seminal MVPA work by Haxby et al. (2001), who found that decoding techniques, unlike univariate analyses, reveal overlapping stimulus representations in the ventral temporal cortex, even though this cortical area was previously thought to contain subregions that only responded to a single stimulus category (i.e., faces and man-made objects such as houses, scissors and chairs). Thus, it appears that information pertaining to individuation and identification is reflected by more subtle changes in BOLD activity, which we were able to detect using MVPA.

There are several other reasons why Xu and colleagues might not have observed an overlap between individuation and identification. First, in the present study participants were required to individuate and identify *each item* within the sample display. By contrast, Xu (2009) had participants judge a test shape based upon its identity only, and not its location. The active involvement of each process in completing the task could have enhanced neural responses associated with individuation and identification. While we cannot say whether the same overlap between object individuation and identification would be observed if we used a pure identification task (e.g., Xu, 2009), our findings do suggest that these processes are reflected in common neural substrates in tasks that require participants to individuate and identify all objects in the display.

Second, we used a longer memory retention period. Xu (2009) had participants maintain sample shapes in memory for only 1 s, and thus activity associated with each VSTM stage was collapsed and finer differences at any given stage could have been temporally smeared. Finally, we analysed activity in a wider set of ROIs. This broader approach ensured a more thorough exploration of individuation and identification processes in the brain, and revealed that signals associated with each of these processes can be detected in a far more distributed neural network.

Results from our recent fMRI study on *temporal* individuation (Naughtin et al., 2013) are consistent with the current findings of involvement of both lower-level perceptual regions and higher-level executive regions in spatial individuation and identification processes. In the previous study, we used a repetition blindness paradigm in which participants had to detect the presence of a scene repetition embedded within a rapid stream of distractors. As participants are typically poorer at individuating an item when it is

preceded by one with the same identity (Kanwisher, 1987; Park & Kanwisher, 1994), we hypothesised that it would be more demanding to successfully individuate two temporally-distinct scenes when they had the same identity (repeated), relative to different identities (non-repeated). Using MVPA, we found activity in the same set of lower- and higher-level regions could discriminate between correctly identified repeated and non-repeated scenes. Thus, even though our previous investigation (Naughtin et al., 2013) and the current study employed paradigms that differed in both task demands and stimulus properties, findings from both point to a common distributed network for identification and individuation in the spatial and temporal domains.

We are not the first to propose a distributed neural network as the underlying neural basis for perceptual or cognitive abilities. For example, in their MVPA study, Vickery, Chun, and Lee (2011) found that reward processes are reflected across many brain regions, yet a smaller, more focal set of regions emerged in the univariate analysis. In addition, Duncan (2010, 2013) has proposed that a large range of cognitive tasks are underpinned by a distributed set of frontal and parietal regions, which he refers to as the *multiple demands* system. These findings underscore the importance of exploring the role of distributed brain regions in any given perceptual or cognitive process.

Conclusion

The present evidence challenges an earlier view that object individuation and identification are subserved by a relatively small set of distinct brain regions (as suggested by Xu, 2009; Xu & Chun, 2009). Both univariate analyses and MVPA suggested that individuation and identification are instead reflected across a larger group of brain regions and that these processes have overlapping neural substrates. We propose that individuation and identification might operate within a distributed neural network in which lower- and higher-level regions communicate. Our findings further indicate that earlier work on the neural bases of object individuation and identification may have been restricted in the number of regions tested and the sensitivity of the data analysis techniques. At the very least, our data illustrates conditions in which the neural object file theory (Xu & Chun, 2009) cannot account for how object individuation and identification are represented in the brain. That is, when the observer must track both the location and identity of objects. Furthermore, we found involvement of these distributed regions varied across different processing stages of VSTM, in a substantial proportion of regions. These results provide new insights into the nature of the neural substrates that give rise to individuation and

identification – two operations that are crucial for a stimulus to reach conscious awareness and be consolidated in VSTM.

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CHAPTER 4: EARLY CORTICAL CONTRIBUTIONS TO OBJECT INDIVIDUATION REVEALED BY PERCEPTION OF ILLUSORY FIGURES

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Abstract

A typical visual scene contains multiple coherent objects distributed across different regions of space. To isolate each object from its surrounds, it must be represented as a stable perceptual entity across both time and space. There has been considerable theoretical debate as to whether this process of *object individuation* occurs pre-attentively or at later attentive stages of visual processing. Moreover, the potential contributions of early sensory areas to object individuation are yet to be determined. Here we used electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) to measure the timecourse of individuation, both for stimuli within and outside the focus of attention, to assess the information processing stage at which object individuation arises, and the extent to which it draws on activity within early visual cortex. We developed a novel paradigm involving items defined by illusory contours, which allowed us to vary the number of to-be-individuated objects while holding the physical stimulus characteristics of the display constant. As early as 100 ms post-stimulus onset, event-related potentials tracked the number of objects in the attended hemifield, but not in the unattended hemifield. Moreover, using multivariate pattern analyses of the fMRI data, we found that area V2 and other extrastriate visual areas were sensitive to the number of individuated objects. We conclude that object individuation of attended items arises at a relatively early stage in the visual information processing hierarchy, and that voluntary spatial attention influences the timecourse of this operation.

To isolate objects in a cluttered visual environment, individuals must first register, or *individuate*, each item as a distinct perceptual entity on the basis of its spatiotemporal properties. Representations generated at this stage of information processing are coarse and are thought to precede analyses necessary for identification (Kahneman, Treisman, & Gibbs, 1992; Pylyshyn, 1994). Functional magnetic resonance imaging (fMRI) studies of the neural substrates of object individuation have implicated a distributed network of occipital, parietal and frontal brain regions (Naughtin, Mattingley, & Dux, in press; Naughtin, Tamber-Rosenau, & Dux, 2013; Xu, 2009). Currently, however, there is no clear picture regarding the temporal dynamics of object individuation, or whether this is influenced by selective attention (Kahneman et al., 1992; Pylyshyn, 1994; Xu & Chun, 2009). Here we used electroencephalography (EEG) to determine the time point at which object individuation arises, for both attended and unattended items. In addition, we employed fMRI and multi-voxel pattern analysis (MVPA) to assess the extent to which object individuation relies upon activity within early sensory brain regions.

Previous EEG studies have found that the number of individuated stimuli in an attended hemifield modulates a lateralized, negative-going event-related potential (ERP) that begins 200-300 ms after stimulus onset (the N2pc component; Ester, Drew, Klee, Vogel, & Awh, 2012; Revkin, Piazza, Izard, Cohen, & Dehaene, 2008). Importantly, N2pc amplitude only increases with target numerosity for sets of four items or less, but not for larger set sizes (Anderson, Vogel, & Awh, 2014; Ester et al., 2012). This component therefore tracks object number only within the established range of *subitizing*, an operation that draws on individuation mechanisms to facilitate rapid and accurate enumeration of distinct items within a display (Piazza, Fumarola, Chinello, & Melcher, 2011; Trick & Pylyshyn, 1994). Although subitizing appears to draw on attentional processes (e.g., Ansari, Lyons, van Eimeren, & Xu, 2007; Cavanagh & Alvarez, 2005; Vetter, Butterworth, & Bahrami, 2010), it is unclear whether individuation, as indexed by subitizing, is evident at time points earlier than the N2pc (but also see, Hyde & Spelke, 2009, 2012; Mazza, Pagano, & Caramazza, 2013), or whether its timecourse is modulated by selective spatial attention.

Here we developed a novel enumeration paradigm that manipulated the number of to-be-individuated items at cued and uncued locations within the left and right visual fields. Each target object was an *illusory* square produced when a quarter segment was briefly removed from each one of a set of four black-disk *inducers* (see Figure 1). Unlike previous paradigms in which displays confounded manipulations of target numerosity with other low-level visual variables, such as hue, luminance or eccentricity, the physical stimuli were

identical across all our numerosity conditions. If object individuation depends upon selective attention, we should observe distinct timecourses for attended and unattended objects. Further, as neurons within the primary visual cortex respond to illusory contours (Murray & Herrmann, 2013), we expected that neural activity associated with individuation should be evident within early sensory cortical areas.

Method and Materials

Participants

The study consisted of three separate experiments. There were 25 participants (18 female) in Experiment 1, the aim of which was to validate the behavioural protocol. There were a further 26 participants (15 females) in Experiment 2, which employed EEG to measure the timecourse of object individuation processes. A subset of 14 participants (9 females) from Experiment 2 also participated in Experiment 3, which employed fMRI to measure patterns of activity across visual cortex associated with object individuation. The mean ages of participants in each of the three experiments were 22.8 years (*SD* = 5.1), 25.5 years (*SD* = 4.4) and 27.4 years (*SD* = 5.4), respectively. Data were excluded from participants with poor task accuracy (three participants in Experiment 1, *n* = 22; two participants in Experiment 2, *n* = 24). All participants had normal or corrected-to-normal vision, gave written, informed consent and were financially reimbursed for their time. The University of Queensland ethics committee approved the experimental protocol.

Design and Stimuli

Placeholder and inducer stimuli consisted of solid black disks (radius of 0.5º of visual angle) superimposed on a light grey background. Inducer disks also contained a gap in one of four quadrants (Figure 1B). These stimuli were presented in groups of four in a square configuration, with a centre-to-centre distance of 1.5º between each disk. Four such configurations were presented in each hemifield (left and right), and the centre of each was 6.2º from fixation. In illusory contour configurations, all four inducers had their gap oriented toward the centre of the configuration. This arrangement created an additional illusory square that was apparent on top of the four black disks (Kanizsa, 1955). These illusory squares served as the objects that participants had to detect. There were also non-illusory configurations in which the inducers were oriented randomly, such that the gap could appear in any one of the quadrants, with the only constraint that no two adjacent inducers ever formed an illusory edge. On any given trial, either side of the array

could contain 0, 1, 2, 3 or 4 new objects (illusory squares), depending on the configuration of the black inducer disks. Critically, the number, shape and positions of the inducer disks remained constant on each side of the display across all trials; only the appearance of one or more illusory squares varied across the trials. We also manipulated covert spatial attention on each trial by cueing participants to one of the two visual hemifields (left or right).

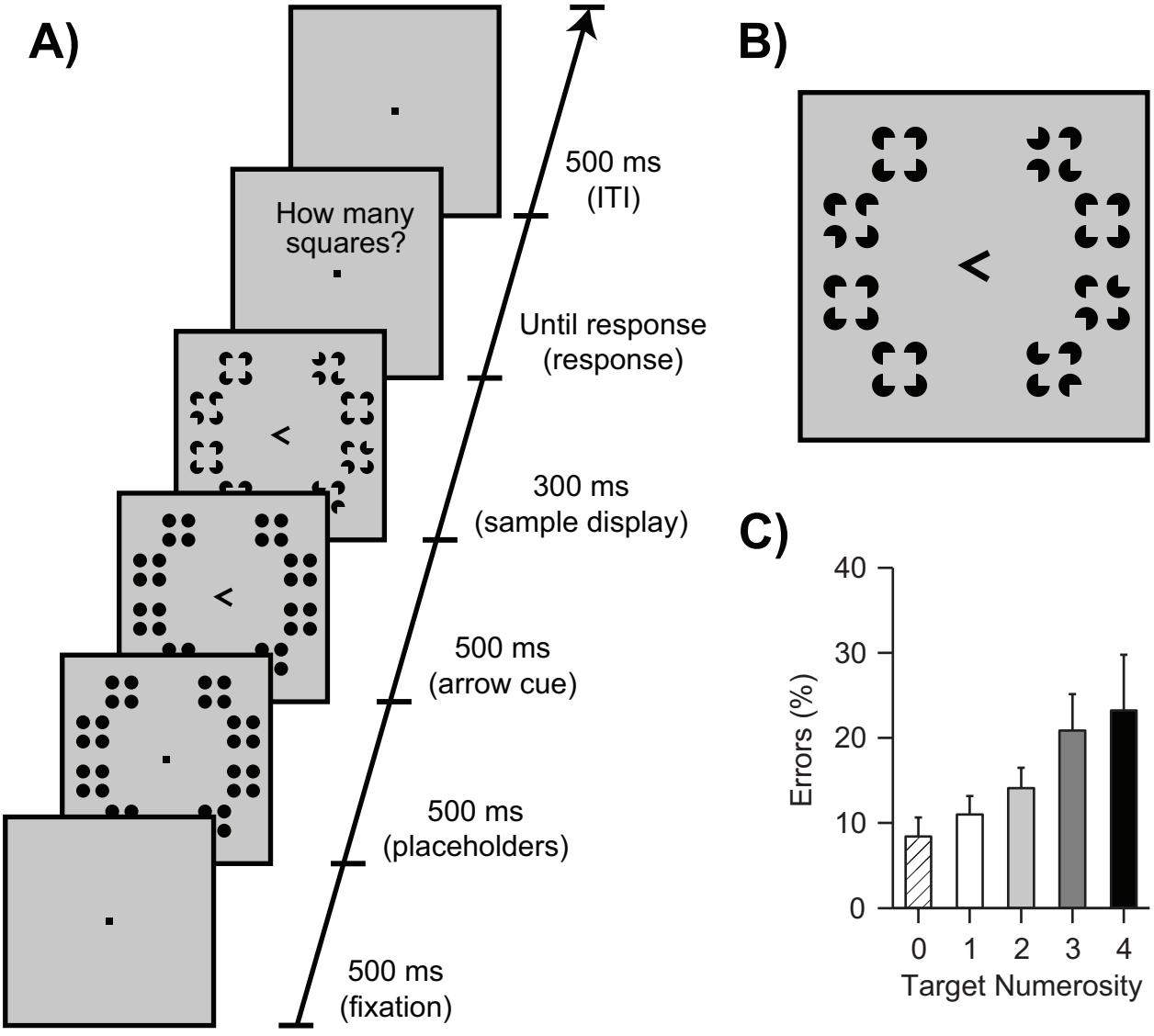

Figure 1. Paradigm and behavioural results for Experiment 1.

(A) Schematic representation of a single trial of the illusory enumeration task. Each trial began with the presentation of four placeholder groups (black disks) in each hemifield, followed by a central arrow cue. The placeholders then changed into inducers (disks with quarter segments removed), where some of the inducer groups were arranged to form an additional illusory square (targets). When prompted, participants reported the number of

targets in the attended hemifield. (B) Example stimulus display in which there are three targets (illusory squares) in the attended hemifield and one to-be-ignored non-target in the unattended hemifield. All remaining placeholder groups contain inducer disks that are oriented such that they do not form any illusory contours. (C) Error rates as a function of the five target numerosity conditions. Error bars represent one standard error of the mean.

In each experiment, there were three within-participant factors: 'Target numerosity' (0, 1, 2, 3 or 4 items), 'non-target numerosity' (0, 1, 2, 3 or 4 items) and 'cued hemifield' (left or right). Target numerosity was the number of illusory squares in the cued hemifield, and non-target numerosity was the number of illusory squares in the uncued hemifield. The cued hemifield was indicated by an arrow cue ('<' or '>') presented in the centre of the screen (1º x 1º). Stimuli were generated in Photoshop and the experiments were programmed in MATLAB using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997).

Procedure

Experiment 1. We first validated our novel enumeration task for manipulating individuation load (Figure 1A). The goal was to employ a paradigm that was similar to standard enumeration tasks in which participants have to individuate a variable number of target items (e.g., Ester et al., 2012; Mazza et al., 2013; Pagano & Mazza, 2012), while controlling for low-level visual features, such as the number of visual elements, hue, luminosity and eccentricity, to ensure visual displays were physically identical across all conditions. Each trial began with a fixation square (500 ms), followed by the presentation of four placeholder configurations in the left and right hemifields (500 ms), each consisting of four black disks. An arrow cue then appeared in the centre of the screen to indicate the visual hemifield to which participants should attend. After 500 ms, each group of placeholder disks then changed to inducer disks by removal of a quarter segment from each. Each configuration within the cued and uncued hemifield could form an illusory square object or a non-illusory configuration (i.e., no illusory square; Figure 1B). This target display remained on the screen for 300 ms, and participants' task was to determine the number of illusory squares that appeared within the *cued* hemifield.

A response screen appeared after offset of the target display, and participants indicated the number of targets via key press. We emphasised response accuracy over speed, and no response deadline was imposed. On any given trial, there could be zero, one, two, three or four targets in the cued hemifield, and the same possible number of ignored non-targets in the uncued hemifield. The next trial began after a 500 ms interval.

Participants completed 100 practice trials, followed by 600 test trials (split across 6 blocks). Response feedback was provided on practice trials only. Trial types were presented in a pseudo-randomised order, and the selection of target/non-target configurations was randomised across trials. Participants were tested in a dimly lit laboratory to minimise distraction from other visual stimuli.

Experiment 2. In Experiment 2, we recorded EEG while participants completed the illusory enumeration task, with the aim of isolating the time point in information processing at which object individuation arises for attended and unattended items. The enumeration task was identical to that described for Experiment 1, with the following exceptions. Each trial began with the cue display for a variable duration of 400-600 ms (the exact duration was randomly determined for each trial), followed by the target display for 300 ms. Cue display duration was jittered to minimise the extent to which any cue-related activity would be present in the ERPs in response to the target display. A response prompt then appeared for 1,700 ms, during which participants had to indicate the number of targets they detected in the cued hemifield. We imposed a response time limit to be consistent with other subitizing ERP studies (e.g., Mazza et al., 2013; Pagano & Mazza, 2012).

To ensure that participants' responses were uniformly distributed over the keyboard, we also assigned arbitrary response keys for each target numerosity ('D' for one target, 'F' for two targets, 'J' for three targets, 'K' for four targets and 'spacebar' for zero targets). Participants responded with the following fingers: left middle, 'D'; left index, 'F'; right index, 'J'; right middle, 'K'; right thumb, 'spacebar.' After the response period, there was a delay of 1,500 ms before the next trial began. Participants completed 800 test trials (split over 8 blocks) and 50 practice trials, and were fitted with a 64-electrode head cap during the practice block. We instructed participants to minimise eye, head and body movements during the experiment, and to take breaks in between each of the testing blocks.

EEG recording. Continuous EEG data were acquired using a BioSemi Active Two system (BioSemi, Amsterdam, Netherlands), digitised at a 1024 Hz sample rate with 24-bit A/D conversion. We recorded from 64 active scalp electrodes mounted on a nylon cap, and these electrodes were arranged according to the International Standard 10-10 system. Electrodes were referenced online to the standard BioSemi reference electrodes. We also recorded eye movements from bipolar horizontal electrooculogram (EOG) using electrodes placed to the outer canthi of each eye, and from the bipolar vertical EOG using electrodes placed above and below the left eye.

EEG analysis. EEG data were analysed offline using Brain Electrical Source Acquisition (BESA 5.3; MEGIS software GmbH, Gräfeling, Germany). Each scalp electrode was referenced offline to the average of all 64 scalp electrodes and subjected to a 0.1 Hz low-pass and a 45 Hz high-pass digital filter. EOG electrodes were referenced offline into bipolar vertical and horizontal EOG channels. Any noisy scalp electrodes identified via visual inspection were replaced by a spherical spline interpolation of voltages recorded at all other scalp electrodes (the maximum number of interpolated electrodes for any given participant was three). The data were segmented into epochs from 100 ms before to 400 ms after the target display onset, and the average voltage recorded 100 ms prior to stimulus onset served as the baseline measurement. Incorrect trials were removed from the ERP analyses (18.1% of trials), due to the unknown source of the error on these trials. We also identified and removed any trials with blinks, eye movements or other artifacts as trials where the difference between the minimum and maximum voltage exceeded 120 μV (a further 1.8% of trials).

The remaining epochs were averaged together, separately for each participant, target numerosity and non-target numerosity conditions (0, 1, 2, 3 or 4 objects). Even though we jittered the duration of the arrow cue over a 200 ms range to cancel out any cue-related activity in the target display ERPs, some residual overlap from the cue ERPs might still have remained. To ensure there was no remaining cue-related activity in the target ERPs, we also subtracted the ERP evoked by zero-target/non-target trials from all other remaining target/non-target numerosities (Busse & Woldorff, 2003). The zero-item trials were identical to the other trial types in terms of the physical stimuli, trial structure, task demands and frequency, except that no illusory squares were presented in the cued and uncued hemifields. This subtraction method effectively removed any activity in the continuous EEG data that were not time-locked to the target display (Talsma & Woldorff, 2005).

Two key components of interest – the P1 and N2 – were identified via visual inspection of the grand average waveform topography maps (Figure 2). For each component, we analysed non-lateralised mean amplitude for the following time windows across a cluster of occipitoparietal electrodes at which the peak was maximal: 100-140 ms for P1 (PO7/PO8 and P7/P8 electrodes) and 185-250 ms for N2 (PO7/PO8 and O1/O2 electrodes). The peaks corresponding to each of these components were calculated from the grand-average waveforms shown in Figure 2A, which reflect the average waveform collapsed across all participants, target numerosity conditions normalised to zero-target trials and non-target numerosity conditions. The mean amplitudes and peak latencies,

collapsed across the two corresponding electrodes for each component, were then subjected to separate one-way repeated-measures analyses of variance (ANOVAs) for the factors of target numerosity (1, 2, 3, 4; collapsed across all non-target conditions) and non-target numerosity (1, 2, 3, 4; collapsed across all target conditions). We conducted separate ERP analyses for targets and non-targets to ensure there were sufficient trial numbers within each cell of the analysis. For all behavioural and ERP analyses, the Greenhouse-Geisser correction was applied for violations of the sphericity assumption.

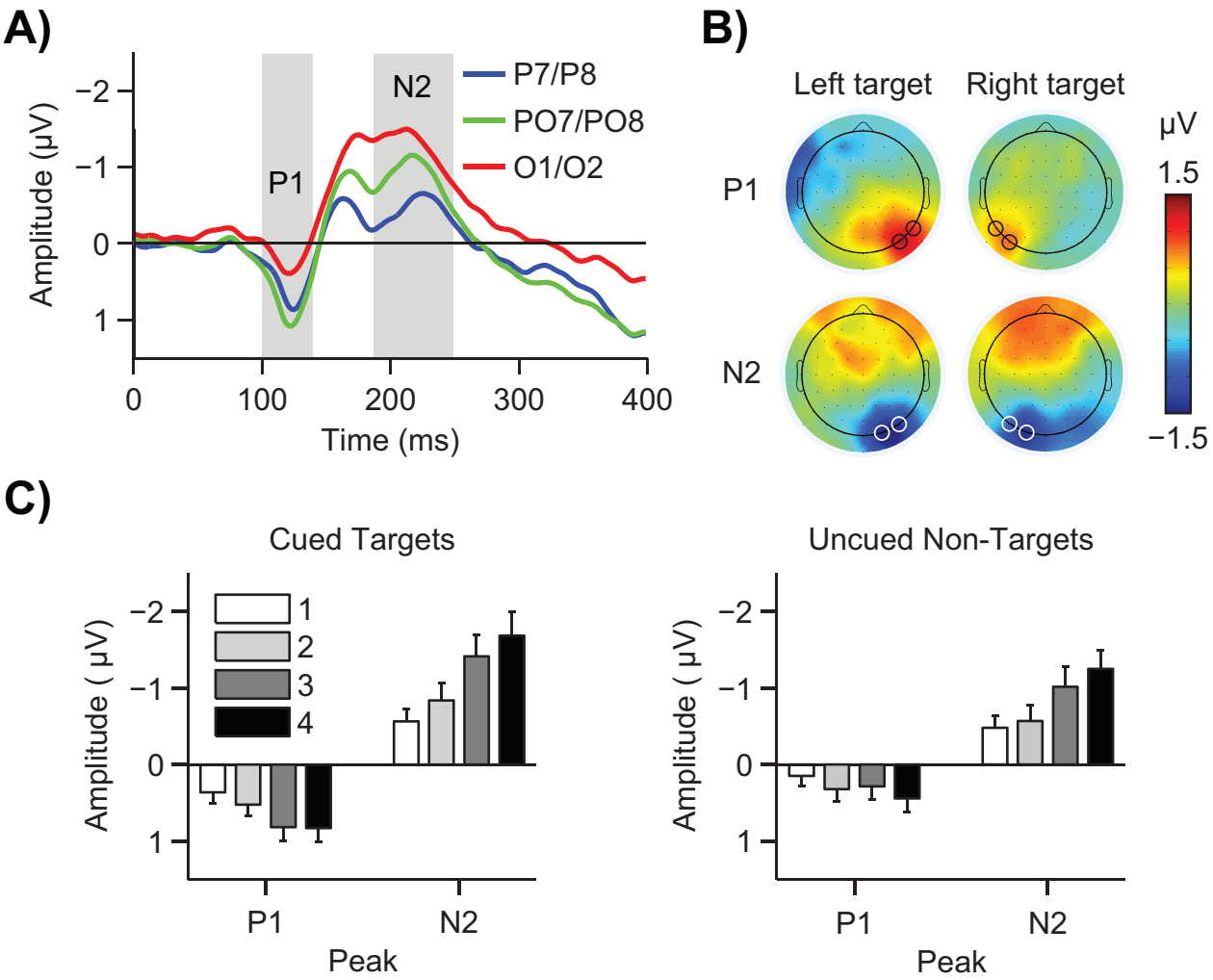

Figure 2. Grand average event-related potentials elicited by different target numerosities in Experiment 2.

(A) Target display event-related potentials (ERPs) averaged across all cued set sizes, recorded at three contralateral occipitoparietal electrodes (P7/P8, PO7/PO8, and O1/O2). These electrodes produced the greatest amplitude either at the early positive (P1; 100-140 ms) or later negative (N2; 185-250 ms) components. The two electrodes with the highest peak amplitude during these time windows were selected for the mean amplitude analysis.

We subtracted the ERP elicited by zero-target (null) trials from the corresponding ERPs under all other target numerosities to remove any residual cue-related activity. (B) Spline-interpolated isocontour voltage topographies at the time corresponding to each peak. These topography maps are averaged across all set size conditions, separately for targets appearing within the left and right hemifield. We also averaged across hemifields for the ERP analysis. Black and white circles indicate which electrodes were used in each peak analysis. (C) ERP peaks as a function of the four target numerosities (1, 2, 3, 4). Error bars indicate one standard error of the mean.

Experiment 3. We followed Experiment 2 with an fMRI study to examine patterns of neural activity associated with object individuation in cortical sensory areas. We employed fMRI because it has superior spatial resolution to EEG, which instead reflects the summed activity recorded across a large number of cortical areas (Luck, 2005). The illusory enumeration task was similar to that used in Experiment 2, with the following changes. The size of all stimuli was reduced by 75% to accommodate the smaller display size inside the scanner, but the relative size of all stimuli was comparable with the previous two experiments. To remove possible carryover effects of the cue to the activity associated with the target display – which likely would have a more prolonged effect given the slow temporal nature of the blood-oxygen-level-dependent (BOLD) signal – we varied the cued hemifield across blocks of eight trials, rather than between trials. There were four blocks in each run, and attention was cued to the left or right hemifield an equal number of times. The arrow cue remained on screen throughout the entire block and enlarged slightly (from 0.75˚ to 1.13˚) for 2 s to alert the participant to the upcoming trial. The target display was then presented for 500 ms, followed by the response screen for 1,500 ms. The response screen now included the placeholder stimuli in both hemifields in addition to the central response prompt. After the response prompt offset and the placeholders remained on screen for the 8 s inter-trial interval. We included the placeholders in the response and inter-trial interval screens to reduce the amount of visual onsets and offsets between each display, which might otherwise have added noise to the fMRI data. We also omitted the set size of four items to ensure we had sufficient trial numbers for each condition when using a slow-event related design; thus, there could be zero, one, two or three illusory square objects presented within the cued or uncued hemifields. Participants responded using a four-button response box in the scanner, and completed seven scanning runs in total.

fMRI acquisition. We used a 3T Siemens Trio MRI scanner (Erlangen, Germany) and a 32-channel head coil to acquire anatomical and functional images. Participants lay

supine in the scanner and viewed the visual display via a rear-projection mirror. We acquired functional T2*-weighted images using a GRE EPI sequence with the following parameters: TR = 2 s, TE = 25 ms, flip angle = 90º, FOV = 192 x 192, matrix = 64 x 64, in-plane resolution = 3 x 3 mm. These images were aligned to the AC-PC plane and consisted of 33 slices with a thickness of 3 mm and a 0.3 mm inter-slice gap. The acquisition of each volume was synchronised with the timing of the stimulus presentation. There were 199 volumes acquired in each run, including 4 initial dummy volumes that were discarded prior to analysis. After the third functional run, a T1-weighted anatomical image was collected using a MPRAGE sequence (TR = 1.9 s, TE = 2.32 ms, flip angle = 9º, FOV = 192 x 230 x 256, resolution = 1 mm^3).

fMRI analyses. All pre-processing steps and analyses were conducted using Brain Voyager QX 2.4 (Brain Innovation, Maastricht, Netherlands) and custom MATLAB code. The data pre-processing steps included 3D motion correction (where each functional image was aligned to the image from the first run), slice-scan time correction and high-pass temporal filtering (three cycles per run). All images were transformed into Talairach space (Talairach & Tourmoux, 1988), and no spatial smoothing was applied to preserve fine-grained spatial information. We used a region of interest (ROI) approach and these ROIs were defined anatomically using the Brodmann (1909) template. We had four ROIs, analysed separately across left and right hemispheres: Primary visual cortex (V1; BA 17), secondary visual cortex (V2; BA 18), extrastriate visual cortex (V3/V4/V5; BA 19) and primary auditory cortex (A1; BA 41). The visual areas were our key ROIs, and A1 was used as a control region to rule out the possibility that some unknown data artifact might have contributed to any observed changes in BOLD activity. As A1 is primarily responsive to auditory information (e.g., Hyde, Peretz, & Zatorre, 2008), it should not be sensitive to the number of visual objects to be individuated.

Data from the fMRI experiment were analysed using MVPA. MVPA has previously been used to show evidence of various perceptual and cognitive operations in early visual areas, such as orientation coding (Haynes & Rees, 2005; Kamitani & Tong, 2005) and the maintenance of information in working memory (Harrison & Tong, 2009), which could not be detected using traditional univariate analyses. This type of analysis examines whether there are subtle changes in the spatial patterns of fMRI activity that can be detected when voxel activity is analysed as an ensemble. MVPA is sensitive to small changes in BOLD activity that are reliable across a cluster of voxels, even if the difference in overall amplitude between conditions is not large enough to be detected in that region (Norman, Polyn, Detre, & Haxby, 2006). Specifically, we trained linear classifiers to discriminate

between patterns of voxel activity for the zero-target trials, compared with the three other target numerosities (1, 2, or 3 objects), yielding three binary comparisons (0 versus 1, 0 versus 2 and 0 versus 3 objects). We also ran an additional analysis that directly tested for an individuation load effect by decoding one-target and three-target conditions. Activity in each ROI was averaged across the time window corresponding to the peak of the BOLD signal (4-8 s after target display onset), transformed into z-scores and mean-centered to remove any overall differences in amplitude between conditions (Naughtin et al., in press; Naughtin et al., 2013).

To ensure any differences between ROIs were not driven by differences in the number of voxels included in the analysis, we only included data from the 100 voxels that showed the greatest overall amplitude, collapsed across the two classifier-conditions. These data were then entered into a linear support vector machine algorithm (Chang & Lin, 2011). We used a leave-one-out classification procedure, whereby one run was reserved to test the generalisation performance of the trained classifier, and the remaining six runs were used to train the classifier. This procedure was repeated seven times such that data from each run were used as the test run once, and classification performance was averaged across all iterations. Significance was tested against chance performance (50%) using a one-sample *t*-test (corrected for multiple comparisons). Our rationale for this analysis was that, if a given region shows evidence of object individuation, it should show improved decoding accuracy with increases in item numerosity.

Results

Behavioural Experiments

Experiment 1. A target numerosity (0, 1, 2, 3, 4) by non-target numerosity (0, 1, 2, 3, 4) repeated-measures ANOVA on the mean proportion of errors revealed a significant main effect of target numerosity, $F(1, 28) = 5.06$, $p = .024$, $\eta_p^2 = .19$, including a significant positive linear trend such that errors increased with larger target numerosities, $F(1, 21) = 6.07$, $p = .022$, $\eta_p^2 = .22$ (Figure 1C). There was no significant effect of non-target numerosity, nor a significant target by non-target numerosity interaction, Fs < 1.09, ps > .370, η_p^2s < .05. These results confirm that the illusory squares produced a subitizing effect analogous to that observed in previous studies (e.g., Ester et al., 2012; Mazza et al., 2013; Pagano & Mazza, 2012).

Experiment 2

Behavioural performance. Consistent with Experiment 1, a repeated-measures ANOVA on the mean proportion errors with factors of target numerosity (0, 1, 2, 3, 4) and non-target numerosity (0, 1, 2, 3, 4) revealed a significant main effect of the former, $F(2, 53) = 7.92$, $p = .001$, $\eta_p^2 = .26$, including a significant positive linear trend, $F(1, 23) = 11.94$, $p = .002$, $\eta_p^2 = .34$. There was no effect of non-target numerosity, $F(4, 23) = 1.73$ $p = .002$, $\eta_p^2 = .34$, but the target by non-target numerosity interaction did reach significance, $F(16, 368) = 2.05$, $p = .010$, $\eta_p^2 = .082$. We followed up this interaction with separate one-way target numerosity ANOVAs conducted on data at each level of non-target numerosity. A significant effect of target numerosity was found for all non-target numerosity ANOVAs, Fs > 3.05, ps < .021, η_p^2s > .12, including a significant positive linear trend, Fs > 4.49, ps < .045, η_p^2s > .16. This result replicates the behavioural performance observed in Experiment 1, again demonstrating a typical subitizing effect. It should be noted that, even though there was also a significant interaction in this experiment, the effect of target numerosity was still evident under all non-target numerosity conditions.

ERP results.

P1. A one-way repeated-measures ANOVA with the factor of target numerosity (1, 2, 3, 4) on mean P1 amplitudes revealed a significant main effect, $F(2, 56) = 5.21$, $p = .005$, $\eta_p^2 = .19$, including a significant positive linear trend, $F(1, 23) = 11.40$, $p = .003$, $\eta_p^2 = .33$. There was no significant main effect when an identical ANOVA was applied to non-target numerosity mean P1 amplitudes, $F(3, 69) = 1.27$, $p = .290$, $\eta_p^2 = .05$. In addition, no significant effects were observed for P1 peak latency measures for either targets or non-targets, Fs < 1.70, ps > .190, η_p^2s < .07. These results suggest that the number of illusory squares in the attended hemifield modulated activity as early as 100-140 ms after target onset, thus, providing the first evidence for object individuation at this early stage of visual information processing.

N2. To assess for later modulations of brain activity associated with individuation, we also conducted separate one-way repeated-measures ANOVAs on mean N2 amplitude for target numerosity (1, 2, 3, 4) and non-target numerosity (1, 2, 3, 4). As was observed for the P1 component, there was a significant main effect of target numerosity, $F(2, 43) = 13.81$, $p < .001$, $\eta_p^2 = .38$, including a significant positive linear trend, $F(1, 23) = 20.09$, $p < .001$, $\eta_p^2 = .47$. There was also a significant main effect of non-target numerosity, $F(3, 69) = 8.10$, $p < .001$, $\eta_p^2 = .26$, as well as a significant positive linear trend, $F(1, 23) = 9.09$, $p < .001$, $\eta_p^2 = .43$. The effect of target numerosity is consistent with previous ERP studies of

object individuation and subitizing, which found enhanced negativity in a similar time window associated with the number of attended targets (e.g., Mazza et al., 2013; Mazza, Turatto, Umiltà, & Eimer, 2007; Pagano, Lombardi, & Mazza, 2014). There were no significant effects for the analysis of peak latency values for either targets or non-targets, *F*s < 1.35, *p*s > .265, η_p^2s < .06.

N2pc. To be consistent with previous ERP studies, we also analysed target- and non-target-related activity for the lateralised N2 component (N2pc). Statistical analyses were performed on mean difference amplitudes and latencies (180-300 ms; time window taken from Mazza and colleagues, Mazza et al., 2013; Mazza et al., 2007; Pagano et al., 2014) after subtracting activity recorded at ipsilateral posterior sites (PO7 and O1 for left targets, PO8 and O2 for right targets) from that recorded at contralateral sites (PO8 and O2 for left targets, PO7 and O1 for right targets). As the N2pc component is a difference waveform, cue-related activity is already partialed out. Thus, for this component only, we did not subtract activity on zero-target trials from the other trial types, allowing us to examine responses on trials in which there were no targets to be individuated.

Separate, one-way repeated-measures ANOVAs on mean N2pc amplitudes with factors of target numerosity (0, 1, 2, 3, 4) and non-target numerosity (0, 1, 2, 3, 4) revealed significant main effects of both target numerosity and non-target numerosity, *F*s > 3.28, *p*s < .015, η_p^2s > .13 (Figure 3A). N2pc amplitude showed a significant positive linear increase with target numerosity, $F(1, 23) = 9.22$, $p = .006$, $\eta_p^2 = .29$, whereas non-target numerosity showed a significant *negative* linear trend, $F(1, 23) = 4.96$, $p = .036$, $\eta_p^2 = .18$. The effect of target numerosity is consistent with prior N2pc investigations into object individuation (Ester et al., 2012; Mazza et al., 2013; Mazza et al., 2007; Pagano et al., 2014), but here we provide the first evidence comparing this with ERP measures of task-irrelevant object individuation. It appears that objects in unattended locations are individuated, but the extent of this processing *declines* with each additional object in the display. We return to this issue in the Discussion.

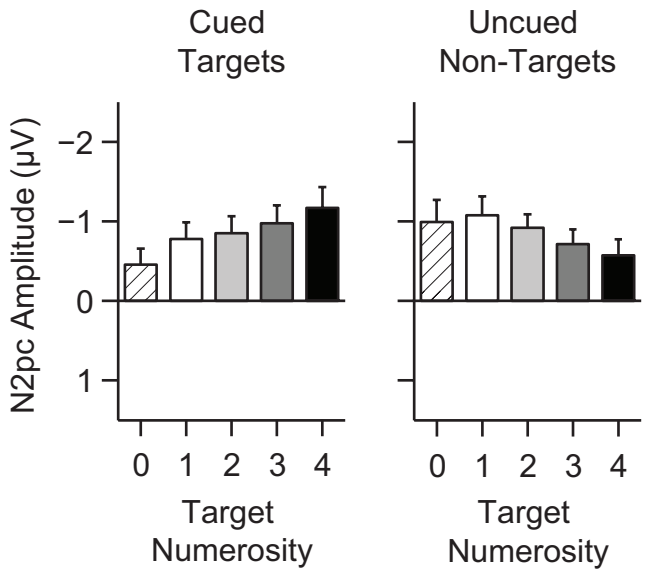

Figure 3. Event-related potential peaks for the N2pc component as a function of target and non-target numerosity.

This component was calculated as a difference waveform between posterior electrodes contralateral, relative to ipsilateral, to the attended hemifield. The plots show mean amplitude across the target (left) and non-target numerosity (right) conditions. Error bars indicate one standard error of the mean.

Experiment 3

Behavioural results. Behavioural performance in the fMRI experiment was comparable to that observed in the previous experiments. A target numerosity (0, 1, 2, 3) by non-target numerosity (0, 1, 2, 3) repeated-measures ANOVA on mean proportion error rates showed a significant main effect of target numerosity, $F(3, 23) = 4.67$, $p = .023$, $\eta_p^2 = .28$, with a marginal positive linear trend, $F(1, 12) = 3.22$, $p = .098$, $\eta_p^2 = .21$. There were no other significant effects or interactions, Fs < 1.30, ps > .244, η_p^2s < .10. These findings confirm that adjustments made to the behavioural paradigm for the purposes of fMRI did not compromise the key behavioural effect.

MVPA results. To be consistent with our ERP approach, we collapsed across the factor of hemifield and assessed whether decoding accuracy was greater than chance for each contralateral and ipsilateral ROI. A series of one-sample *t*-tests (corrected for the statistical tests conducted across each region, hemisphere and classifier comparison; minimum $p = .002$) revealed that activity in V1 could not be decoded across any of the classifier comparisons, ts > 3.35, ps > .168, with the exception of the zero-versus-two comparison for ipsilateral V1, $t(13) = 7.10$, $p = .019$ (Figure 4). Classifiers could not

discriminate between zero- versus one-target conditions in V2 or V3/V4/V5 activity, *t*s > 2.83, *p*s > .453, but activity in these bilateral regions could distinguish zero-target trials from both two- and three-target trials, *t*s > 7.10, *p* < .001. Moreover, the direct comparison between one-target and three-target trials also revealed significant decoding bilaterally in V2 and V3/V4/V5 (minimum decoding accuracy = 62.7%), *t*s > 8.72, *p*s < .001. These decoding results therefore suggest that activity in visual areas as early as V2 tracks the number of individuated targets, and that this bilateral activity reflects a plausible source of modulation observed in the P1 component in Experiment 2. There were no significant differences in decoding for contralateral and ipsilateral regions for any of the ROIs, *t*s < 3.04, *p*s > .302. To confirm that the significant decoding we observed was specific to object individuation and did not simply reflect some artifact of our design, data or analyses, we also assessed decoding accuracy in two control regions – contralateral and ipsilateral A1. Activity in these regions could not be discriminated between the conditions for any of the comparisons, *t*s > 3.50, *p*s > .125, suggesting that the above-chance decoding observed for V2 and V3/V4/V5 reflects a genuine effect of object individuation load.

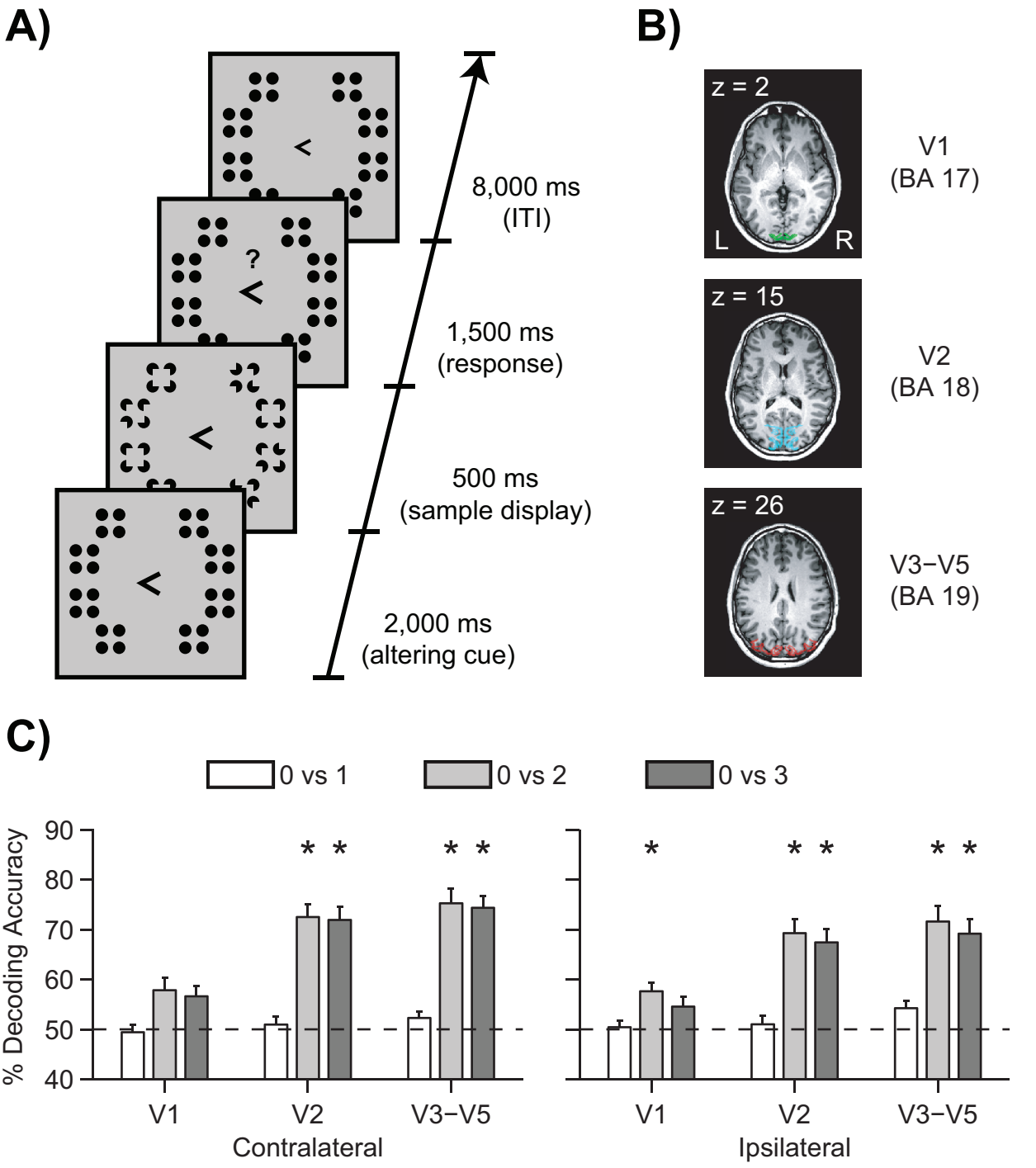

Figure 4. Paradigm and multi-voxel pattern analysis results for Experiment 3.
(A) Schematic representation of a single trial of the slow-event related illusory enumeration task. Similar to the paradigm used in Experiment 1, participants were first presented with the placeholder display with a central arrow cue (cued hemifield was now blocked across each experimental run). The placeholders then changed into inducers and participants had to indicate the number of new objects (illusory squares) that appeared in the attended hemifield. There was an extended inter-trial interval (ITI), following a standard slow-event related design. (B) Anatomical regions of interest (ROIs) defined using the Brodmann

areas (BA) atlas. These ROIs correspond to primary visual cortex (V1; BA 17), secondary visual cortex (V2; BA 18) and extrastriate visual cortex (V3-V5; BA 19). (C) Decoding accuracy results from the multi-voxel pattern analyses conducted on each ROI in the hemisphere contralateral and ipsilateral to the attended hemifield. Classifiers were trained to discriminate between zero-target trials and each of the other target numerosities separately. Dashed lines indicate chance performance and the asterisk (*) denotes accuracies greater than chance performance, corrected for multiple comparisons. Error bars represent one standard error of the mean.

Discussion

Here we examined the temporal dynamics of individuation for attended and unattended objects, and the extent to which this operation relies on activity within sensory processing regions of the brain. We employed a novel enumeration paradigm in which identical inducers (black disks with quarter segments removed) either did or did not form illusory squares. Critically, this design kept visual elements constant across numerosity conditions (zero to four illusory squares), which allowed us to explore early cortical contributions to object individuation in the absence of other confounding physical variables (e.g., changes in hue or luminance as a function of numerosity). We observed that the number of attended targets modulated EEG activity as early as 100 ms post-stimulus onset. This finding suggests that object individuation occurs early in the visual information processing hierarchy for attended targets (Johannes, Münte, Heinze, & Mangun, 1995). In the fMRI experiment, we also found evidence of individuation in sensory processing regions of visual cortex (V2 and extrastriate visual areas). Specifically, activity in these areas discriminated between conditions in which two or three targets were individuated, relative to no objects, and between conditions of low (one target) and high (three targets) individuation load. We speculate that activity within these brain areas reflects the source of the set-size-modulation of the P1 observed in our EEG experiment.

We also found evidence that unattended, task-irrelevant items are individuated, but that this operation has a later temporal signature than that for attended objects; specifically, the number of unattended non-targets only modulated the N2 component, not the P1. These findings show, for the first time, that distractor objects are indeed individuated, but not at the same time point or in the same manner attended targets. This suggests a key role of attention in the timecourse of operations involved in the registration of stimuli as distinct objects, and is consistent with attentive accounts of object individuation (Kahneman et al., 1992; Xu & Chun, 2009), and previous studies

demonstrating the influence of attention on subitizing (e.g., Ansari et al., 2007; Cavanagh & Alvarez, 2005; Vetter et al., 2010). Crucially though, here we show the time window at which this effect arises. Specifically, when we considered the lateralised difference in N2 amplitude, we found the N2pc component decreased in negativity with non-target numerosity, which contrasted with the positive linear relationship between target numerosity and N2pc amplitude observed for attended objects. This latter result is consistent with previous ERP studies of subitizing (e.g., Ester et al., 2012; Mazza et al., 2013). Although our study was not designed to directly assess interactions between the individuation of targets and distractors, the differing N2pc patterns observed for each might reflect that distractor individuation depends on the number of targets that must be concurrently individuated. This interpretation is consistent with this operation being severely capacity-limited (Pylyshyn, 1994; Xu & Chun, 2009). Given that an fMRI study by Jeong and Xu (2013) found evidence of distractor individuation under low, but not high, target encoding loads, one would predict that N2pc amplitude might interact in a similar way.

The time window (P1, 100-140 ms) in which we observed evidence for object individuation is much earlier than has been previously reported in subitizing studies. For example, Hyde and Spelke (2009, 2012) had participants passively view a variable number of dots within a small (1, 2, 3) or large set size (8, 16, 24). These authors observed a negative-going potential that peaked 139-199 ms after stimulus onset, and that increased with target numerosity for small set sizes (i.e., within the subitizing range), but not large set sizes. This finding suggests that object individuation occurs within the first 200 ms after stimulus onset. However, this conclusion was challenged by Mazza et al. (2013), who found no effect of numerosity when targets appeared amongst distractors, which effectively equated the total number of visual elements across numerosities (see also, Gebuis & Reynvoet, 2012; Libertus, Woldorff, & Brannon, 2007). But, the conclusions of Mazza et al. (2013) are not definitive, as low-level properties of the displays differed between individuation loads in this study (the targets were defined as a unique colour relative to distractor items). We overcame this issue by implementing a novel paradigm in which all sensory properties were balanced across target conditions, yet the number of separate target objects (illusory squares) could be systematically manipulated across trials. In addition, we found converging evidence for an early onset of this individuation effect in Experiment 3, in which the number of target objects could be decoded in V2 and extrastriate visual areas.

It is worth noting an ERP study by Anderson, Vogel, and Awh (2013), in which target numerosity was also manipulated under conditions that kept the physical input constant. In this study, participants were presented with a target display containing two pairs of circular inducers with a square gap missing from one side. Inducers in both pairs were either oriented toward each other to form an illusory rectangle (the 'grouped' condition) or oriented randomly (the 'ungrouped' condition). Participants' task was to remember the orientation of each individual inducer (i.e., the illusory shape itself was task-irrelevant). Anderson et al. found that N2pc amplitude was reduced in the grouped relative to the ungrouped condition. Similar findings have been reported using fMRI, in which individuation-related brain regions are less active for grouped objects than ungrouped objects, suggesting that grouping cues can enhance the amount of information encoded in memory (Xu, 2008; Xu & Chun, 2007). In the present study, the illusory contours formed additional target items and were therefore integral, rather than incidental, to participants' task. Put differently, our results reflect a measure of the number of perceived objects, rather than a measure of the number of physical objects under grouped or ungrouped contexts.

In conclusion, we have shown that object individuation of attended items arises 100 ms after stimulus onset (P1), suggesting that this operation occurs earlier in the visual information processing hierarchy then previously proposed. Our ERP evidence was corroborated by fMRI results, which showed that the number of attended targets could be decoded in early visual cortex, including V2 and extrastriate visual areas (V3-V5). Moreover, we found that unattended items are individuated, but at a later time point (N2), demonstrating that selective attention impacts the temporal dynamics of individuation. These findings extend our earlier fMRI work (Naughtin et al., in press; Naughtin et al., 2013) by showing evidence of object individuation in brain areas that are earlier in the visual processing hierarchy than previously explored. Collectively, by controlling for low-level visual differences between numerosity conditions, and employing neuroimaging techniques with high temporal (EEG) and spatial (fMRI) resolution, we have uncovered differences in the temporal dynamics associated with the individuation of attended and unattended objects, and have demonstrated the role of early sensory brain regions in this operation.

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CHAPTER 5: GENERAL DISCUSSION

Summary of Research Findings

The overarching aim of this thesis was to examine the cognitive and systems-level neural mechanisms involved in registering objects as distinct events across time and space. Specifically, I explored the brain regions that support spatio-temporal object individuation, at initial perceptual stages of information processing and those involved in encoding, maintenance and retrieval stages of visual short-term memory. In addition, I investigated how object individuation interacts with identification processes in the brain, and the timecourse associated with this operation. These research questions were addressed using a range of behavioural paradigms and neuroimaging techniques (with multiple analytic approaches).

The study reported in Chapter 2 (Naughtin, Tamber-Rosenau, & Dux, 2013) had two key aims: To isolate the brain regions that are involved in successfully individuating objects during perception on the basis of temporal information alone, and the neural consequences that arise when individuation reaches its capacity limit (as reflected in repetition blindness, RB). During functional magnetic resonance imaging (fMRI), participants completed a rapid serial visual presentation (RSVP) task designed to elicit RB – a reduced ability to report the second of two repeated items when they appear close together in time. RB is hypothesised to reflect a failure of object individuation, such that the second repeated item is not registered as a separate occurrence to the first, and hence does not enter consciousness. It has been proposed that this failure of perceptual awareness arises due to a temporal limit in the number of distinct items (tokens) that can be linked with the same identity representation (type; see also, Chun, 1997; Kanwisher, 1987; Wyble, Bowman, & Nieuwenstein, 2009).

I compared correct and incorrect instances on repeated and non-repeated trial types to isolate temporal individuation and RB. For temporal individuation, I found that trials where observers correctly reported the appearance of a repetition (high individuation load) compared with those in which they correctly reported a non-repetition (low individuation load) elicited distinct patterns of activity across a large set of occipital, frontal and parietal brain regions. This finding suggests that temporal individuation relies upon a wide range of ‘lower-level’ perceptual and ‘higher-level’ attentional and executive brain regions. The distributed nature of this activation pattern is in line with existing models of consciousness (Baars & Franklin, 2003; Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001), which argue that a diffuse set of brain regions contributes to processes that give rise to awareness. Second, in response to the capacity limits of individuation, I found the left premotor cortex was more active to missed than to seen

repetitions, suggesting that this region is implicated in the processing limitations that give rise to RB. Collectively, the results reported in Chapter 2 provide the first indication of the neural substrates of temporal individuation and RB.

The experiments reported in Chapter 3 explored the extent to which object individuation and object identification draw on overlapping neural substrates during encoding, maintenance and retrieval stages of visual short-term memory (Naughtin, Mattingley, & Dux, in press). According to the neural object file theory (Xu, 2009; Xu & Chun, 2009), object individuation and identification are underpinned by distinct brain regions; the inferior intra-parietal sulcus (IPS) is involved in the former, and the superior IPS and lateral occipital complex in the latter. To test this proposed neural dissociation at the level of encoding and beyond, I scanned participants using fMRI while they viewed displays consisting of one shape, four identical shapes or four different shapes. Participants were instructed to remember the location and identity of these items over a relatively long retention interval to isolate the different short-term memory stages.

Using the same comparisons as Xu (2009), brain regions involved in individuation were defined as those that distinguished between one object and four identical objects (reflecting changes in the number of objects only). On the other hand, identification areas were characterised as being sensitive to differences between four identical versus four different objects (reflecting changes in the number of object identities only). Consistent with Xu and Chun's (2009; Xu, 2009) proposal that individuation and identification have distinct neural substrates, I found some brain regions that were uniquely responsive to one of these operations. However, this hypothesis did not hold across all the brain regions examined, as other areas reflected both processes. This overlap between brain regions involved in individuation and identification processes was evident in both lower- and higher-level cortical areas, either at the same or different stages of visual short-term memory. These findings challenge the dissociation proposed by Xu and Chun in the neural object file theory, and instead implicate a common set of brain regions in object individuation and identification. In addition, the distributed neural areas implicated in spatial individuation in Chapter 3 are consistent with the temporal individuation results reported in Chapter 2 (Naughtin et al., 2013).

The experiments presented in Chapter 4 aimed to characterise the timecourse of object individuation to determine the stage of processing at which this operation arises for attended and unattended items, and the extent to which it draws on early sensory brain areas. This study was motivated by previous work that had linked the N2pc component with subitizing – the ability to rapidly and accurately enumerate a small set of items, which

draws heavily on individuation processes (Piazza, Fumarola, Chinello, & Melcher, 2011; Trick & Pylyshyn, 1994). Typically, increasing the number of individuated objects within the subitizing range (up to four items) enhances N2pc amplitude (e.g., Ester, Drew, Vogel, & Awh, 2012; Mazza, Pagano, & Caramazza, 2013; Pagano, Lombardi, & Mazza, 2014), an event-related potential that is often linked with shifts of spatial attention (Jolicœur, Brisson, & Robitaille, 2008; Luck & Hillyard, 1994). Evidence for the same set-size modulation at earlier event-related potentials is mixed (Hyde & Spelke, 2009, 2012; Mazza et al., 2013), however, and these conclusions were hindered by the fact that manipulations of object individuation load (i.e., the number of target items) was confounded with other low-level visual factors (e.g., the total number of visual elements, hue, luminosity, etc.). Moreover, theoretical accounts differ in terms of whether object individuation arises pre-attentively (Pylyshyn, 1994), or at later attentive stage of processing (Kahneman, Treisman, & Gibbs, 1992; Xu & Chun, 2009), but this is yet to be directly tested (but also see, Jeong & Xu, 2013). I explored the temporal dynamics of individuation are influenced by selective attention by comparing the timecourses associated with the individuation of task-relevant and irrelevant objects.

To explore the timecourse of object individuation, I recorded electroencephalography (EEG) during a novel enumeration paradigm, in which participants had to individuate up to four target items (i.e., within the subitizing range). Importantly, this task removed low-level visual differences between numerosity conditions by using illusory targets created by identical inducing stimuli. Both the P1 (sensory processing) and N2 (perceptual encoding) components reflected the number of attended targets, whereas the number of unattended non-targets was only evident at the level of the N2. Convergent evidence for the early locus of target-related individuation was found using fMRI. Activity in early visual areas, including V2, varied as a function of the number of individuated targets. I hypothesised that these early visual areas might have generated the P1 effect observed for attended targets in the EEG experiment. These findings suggest that object individuation occurs at an early stage of information processing. Furthermore, as unattended items are individuated at a later stage of analysis, this suggests that voluntary spatial attention modulates the timecourse of this operation.

Implications of Research Findings

As noted above, the findings reported in Chapters 2 and 3 – which demonstrate that the neural substrates for object individuation are distributed across the brain – have important implications for the dominant cognitive-neuroscientific account of object

individuation (Xu & Chun, 2009). Xu and Chun have proposed a key role of the inferior IPS in object individuation, and that this brain area is distinct from of those that support object identification, and vice versa. The present data, however, suggest that object individuation and identification are distributed and overlapping processes in the brain. It is important to note that this neural overlap does not necessarily suggest that these two cognitive processes interact directly, but rather that activity associated with individuation and identification can be detected in common brain regions. Support for the hypothesis that individuation and identification might draw on common resources, however, comes from behavioural experiments that have shown that these two operations can interfere with each other. For example, Piazza et al. (2011) found the number of separate identities held in memory correlates with, and can impair (in a dual-task setting), the number of items that observers can simultaneously subitize. Thus, future theoretical work on object individuation and its neural bases will need to consider this process from a systems-level approach, beyond the current focal regions it is implicated in, and account for how it relates to identification operations.

It is worth noting the large number of regions of interest and multiple analytic approaches used in the fMRI investigations reported in this thesis. In previous studies, object individuation was only ever probed in three regions across the occipital and parietal lobes, which restricted the search for the neural substrates of this process to these brain areas. This type of 'divide and conquer' approach is not uncommon in cognitive neuroscience because it is focused and hypothesis-driven, but it does come with the risk of possibly missing the involvement of a larger set of brain areas (see, Vickery, Chun, & Lee, 2011). Moreover, evidence of object individuation was previously only assessed on the basis of gross changes in blood oxygen level dependent (BOLD) amplitude (that is, a conventional univariate analysis approach). But univariate, activation-based analyses are only one way to assess changes in BOLD signals across experimental conditions. By employing a multivariate approach – specifically, multi-voxel pattern analysis – along with univariate analyses, I was able to identify brain regions displaying both relative differences in their level of activation, as well as others with distinct activity patterns, in response to the experimental manipulations (Norman, Polyn, Detre, & Haxby, 2006; Tong & Pratte, 2012). The combination of these multiple analytic approaches afforded a more thorough exploration of the extent to which a given cognitive operation is reflected in the brain.

The experiments presented in this thesis employed a range of behavioural paradigms to investigate object individuation: Repetition blindness (Chapter 2), visual short-term memory (Chapter 3) and enumeration (Chapter 4). It is important to study

cognitive processes using a variety of approaches, as this allows one to demonstrate that effects generalise and are not simply a reflection of a specific stimulus-response pairing. These paradigms likely tapped different aspects of individuation, such as the specific stage of processing, but they nonetheless help form a coherent picture of this operation. For instance, while the RB paradigm likely tapped an early perceptual locus of individuation, and the visual short-term memory paradigm probably reflected later stages, the regions implicated in object individuation largely overlapped. This consistency suggests the involvement of a common individuation mechanism across both tasks. Furthermore, a recent review of electrophysiological work by Anderson, Vogel, and Awh (2014) suggests a similar task-independent relationship between the N2pc component and subitizing. These authors propose that what is common across these tasks is an individuation mechanism that determines the capacity of subsequent processing stages. Object individuation could therefore act as a core gating mechanism for a range of cognitive operations in vision.

The results presented in this thesis raise important considerations for how object individuation is operationalized. A standard approach for manipulating object individuation load is to vary the physical number of items (e.g., Xu, 2009) or number of distinct-coloured items in a display (e.g., Ester et al., 2012; Mazza et al., 2013); the more target items there are, the higher the individuation load. For example, Mazza et al. (2013) used displays that consisted of a variable number of red shapes (targets) presented among green shapes (distractors). The problem with these types of tasks is that they confound changes related to object individuation with numerous other low-level stimulus factors (e.g., the total amount of visual information, hue, luminosity, etc.). I ruled out the influence of such factors using various approaches in this thesis. For instance, in Chapter 2, I conducted an additional control analysis on conditions that differed in stimulus properties (e.g., repeated scenes versus non-repeated scenes), but kept individuation load constant. Despite the fact that this stimulus control analysis was substantially more powerful than the key analysis that manipulated temporal individuation load, I did not find any significant decoding in the control analysis, as predicted. I addressed this issue more directly in Chapter 4 by developing a paradigm that eliminates these visual confounds entirely by using illusory target stimuli. The physical stimuli were therefore constant across all numerosity conditions, meaning that any early perceptual effects could not have been driven by lower-level sensory properties. This paradigm presents a novel way to isolate and manipulate object individuation.

Future Research Directions

The experiments reported in Chapter 2 used RB as a measure of the temporal capacity limits of object individuation, but there are other paradigms that might also tap a similar processing limit. One of these phenomena is object substitution masking (OSM). In the standard task used to elicit this effect, an array of items is presented (e.g., circles with a gap on one side). A four-dot mask is presented around one of the items and this item is denoted as the target. The critical manipulation is the offset of the four-dot mask: The mask either offsets simultaneously with the entire array, or is delayed relative to the rest of the stimulus array. Participants are typically poorer at reporting the target item when the mask's offset is delayed, relative to when it is simultaneous, with the target (the OSM effect), and this deficit is thought to reflect a failure of perceptual consciousness (Di Lollo, Enns, & Rensink, 2000). According to Lleras and Moore (2003; Moore & Lleras, 2005), when the target and mask first appear together, a token is created for their spatial location. Relevant featural information for both items is then linked to this single representation. When the target offsets and the mask remains on the screen, however, the object representation is updated such that it now only includes the featural information corresponding to the mask. Thus, the necessary target information does not reach awareness and is no longer available for conscious report.

Whereas RB represents a failure to individuate two targets as distinct items, OSM reflects an inability to individuate a target as a distinct item from its mask. This account by Lleras and Moore is similar to that proposed in Di Lollo, Enns, and Rensink's (2000) re-entrant theory. Di Lollo et al. argue that when the target and mask first appear together, a fleeting representation of this combined stimulus is created in lower-level brain areas and then fed forward to higher anterior brain regions for further processing and consolidation. Because of the brief nature of the stimulus exposure, the initial representation sent to anterior brain areas is coarse and incomplete and, via re-entrant processing, must be checked against information present in lower-level areas to develop a more durable representation. If the mask remains on screen after the target has offset, however, there will be a mismatch between the representations present in lower areas (mask alone) and higher areas (combined mask and target). Thus, the initial representation is substituted with the new representation, effectively discarding any information about the target. Like this account of Di Lollo et al., Lleras and Moore suggest that the initial mask-target representation is updated to include only mask information, but they provide more detail about the specific manner in which the mask gets substituted for the target (Guest, Gellatly, & Pilling, 2012).

Future research could investigate whether RB and OSM tap the same capacity limits of individuation at the behavioural level and, if that is the case, how this overlap is reflected in the brain. It would also be interesting to examine how limitations of object individuation relate to other perceptual deficits like the attentional blink. At least behaviourally, the evidence suggests that RB and the attentional blink can be dissociated (Chun, 1997; Dux & Marois, 2007; Ward, Duncan, & Shapiro, 1997), but these two processing limitations are yet to be examined concurrently in the brain. The results from Chapter 2 suggest that the attentional blink and RB might have dissociable neural substrates, but the tasks used in this experiment and those used to investigate the attentional blink (e.g., Marois, Yi, & Chun, 2004) are too dissimilar to make any strong conclusions. This research question could be addressed directly using a single paradigm that can elicit both deficits, like the RSVP tasks used by Chun (1997) and Dux and Marois (2007).

Experiments described in Chapters 2, 3 and 4 implicate a widespread network of brain areas in object individuation, but it is unclear how these areas are coordinated, or whether they form a single network or multiple networks. Future research could therefore investigate functional relationships between brain areas during object individuation. The use of connectivity analysis techniques, such as psychophysiological interactions (Friston et al., 1997), dynamic causal modelling (Friston, Li, Daunizeau, & Stephan, 2011), independent component analysis (Hyvarinen, 1999) or Granger causality (Granger, 1969), would provide insights into how information is transferred between individuation regions, and which brain regions directly or indirectly influence each other.

For example, it would be interesting to explore the dynamics of the object individuation network across different processing stages. The findings from Chapter 3 suggest that brain regions that reflect individuation vary across encoding, maintenance and retrieval stages of visual short-term memory, suggesting that different brain regions might be active depending on specific processing demands. The use of connectivity analyses could also shed light on how brain regions associated with object individuation are related to those involved in object identification. Gazzaley, Rissman and D'Esposito (2004) have used this approach to examine the functional relationship between brain regions during working memory maintenance. These authors found that activity in a distributed network of frontal, parietal, occipitotemporal and subcortical areas was significantly correlated with responses in the fusiform face area (defined as the seed region) during the maintenance period. These findings not only implicate a distributed set

of brain regions in working memory maintenance, but also demonstrate the functional connections within this network.

The experiments presented in this thesis focused on the relationship between functional changes in the human brain and object individuation, but it is also highly likely that structural brain characteristics are linked with this cognitive operation. Indeed, structural differences might help determine why some people have a larger individuation capacity than others (for an example of such individual differences, see Piazza et al., 2011). One avenue for future research would be to examine the role of white matter integrity in individuation. Because the global workspace model of consciousness implicates a distributed network of brain regions that communicate with each other via long-range connections (Baars & Franklin, 2003; Dehaene et al., 1998; Dehaene & Naccache, 2001), one might predict that conscious awareness should depend upon white matter integrity (Reuter et al., 2009). In support of this hypothesis, Reuter et al. (2009) found that patients with multiple sclerosis – an autoimmune disorder that is characterised by damage to white matter fibres (Au Duong, Audoin, et al., 2005; Au Duong, Boulanouar, et al., 2005; Cader, Cifelli, Abu-Omar, Palace, & Matthews, 2006) – required a longer delay between the onset of a target and subsequent mask before they could consciously report it. In addition, white matter density has been associated with the development of working memory capacity (Klingberg, 2006), and normal age-related declines in working memory performance (Kennedy & Raz, 2009). Given the associations between structural differences in white matter tracts and these cognitive operations, future work could explore the relationship between structure (e.g., white matter integrity) and object individuation performance. This research question could be addressed either using diffusion tensor imaging to measure white fibre tracts in healthy adults, or by testing clinical populations who show declines in white matter density.

Future work might further explore the nature of distractor-related individuation. Findings from Chapter 4 suggest that distractors that appear in unattended spatial locations can be individuated, but that this process occurs at a later stage than that for attended stimuli. Although these results suggest that selective attention mechanisms play a role in object individuation (Kahneman et al., 1992; Xu & Chun, 2009), it is unclear whether distractor-related individuation can be eliminated completely. Does object individuation operate in an automatic, pre-attentive manner, as was originally proposed by Pylyshyn (1989), such that objects outside the focus of attention are spontaneously indexed for further analysis? Results from Jeong and Xu (2013) suggest that distractors can be individuated automatically, but only when there is a small number of targets to be

encoded. Specifically, even when locations of upcoming targets are pre-cued (to direct attention to relevant locations; Posner, 1980), the inferior IPS is more active to targets in the presence of distractors than to targets alone. Here activity in the inferior IPS was taken as a proxy for object individuation processes, and thus, these findings do not characterise the nature of this operation in other brain regions; nor does fMRI provide the necessary temporal resolution to detect whether an attentional cue influences the timecourse of distractor-related individuation. Future work could use the paradigm introduced in Chapter 4, with an additional cueing component, to explore whether the timecourse of distractor-related individuation is influenced when attention is pre-cued to target locations, and how such pre-cueing affects the corresponding neural processes.

Conclusions

Object individuation is an important cognitive process that allows an observer to effectively parse discrete stimuli in a visual scene, so that these representations can undergo further featural analysis. In this thesis, I found that both the temporal and spatial components of individuation can be detected across a common, distributed set of cortical regions, some of which overlap with identification processes. I also found that object individuation occurs relatively early in visual processing, and that selective attention plays a role in determining which items are indexed in this process. Overall, the results presented here provide novel insights into how object individuation is implemented in the human brain, the neural consequences that arise when its capacity limits are exceeded, and its temporal dynamics.

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APPENDIX A. THE NEURAL BASIS OF TEMPORAL INDIVIDUATION AND ITS CAPACITY LIMITS IN THE HUMAN BRAIN

Naughtin, C. K., Tamber-Rosenau, B. J., & Dux, P. E. (2013). The neural basis of temporal individuation and its capacity limits in the human brain. *Journal of Neurophysiology, 111*(3), 499-512. doi: 10.1152/jn.00534.2013.

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The neural basis of temporal individuation and its capacity limits in the human brain

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Naughtin CK, Tamber-Rosenau BJ, Dux PE. The neural basis of temporal individuation and its capacity limits in the human brain. *J Neurophysiol* 111: 499–512, 2014. First published November 6, 2013; doi:10.1152/jn.00534.2013.—Individuation refers to individuals' use of spatial and temporal properties to register an object as a distinct perceptual event relative to other stimuli. Although behavioral studies have examined both spatial and temporal individuation, neuroimaging investigations of individuation have been restricted to the spatial domain and at relatively late stages of information processing. In this study we used univariate and multivoxel pattern analyses of functional magnetic resonance imaging data to identify brain regions involved in individuating temporally distinct visual items and the neural consequences that arise when this process reaches its capacity limit (repetition blindness, RB). First, we found that regional patterns of blood oxygen level-dependent activity in a large group of brain regions involved in "lower-level" perceptual and "higher-level" attentional/executive processing discriminated between instances where repeated and nonrepeated stimuli were successfully individuated, conditions that placed differential demands on temporal individuation. These results could not be attributed to repetition suppression, stimulus or response factors, task difficulty, regional activation differences, other capacity-limited processes, or artifacts in the data or analyses. Consistent with the global workplace model of consciousness, this finding suggests that temporal individuation is supported by a distributed set of brain regions, rather than a single neural correlate. Second, conditions that reflect the capacity limit of individuation (instances of RB) modulated the amplitude, rather than spatial pattern, of activity in the left hemisphere premotor cortex. This finding could not be attributed to response conflict/ambiguity and likely reflects a candidate brain region underlying the capacity-limited process that gives rise to RB.

individuation; consciousness; repetition blindness; multivoxel pattern analysis; attention

BEHAVIOR IS SHAPED by how individuals perceive their external environment. Because our environment provides far too much sensory information for all of it to be processed up to awareness, we rely on selective attention mechanisms to reduce the overwhelming amount of available information to a manageable set of relevant items and/or sources (Pashler 1998). Merely attending to sensory information, however, does not guarantee that it will reach awareness or impact behavior, because such information needs to be encoded in relation to the observer's preexisting rules, goals, and knowledge (Cohen et al. 2012).

In vision, a key operation implicated in successful object encoding is "individuation," the process by which observers use spatial and temporal episodic cues to determine where and when an object appeared (e.g., Chun 1997; Kahneman et al. 1992; Mitroff et al. 2007; Pylyshyn 1989, 1994; Xu and Chun 2009). This process is crucial for registering individual items as distinct perceptual events and is thought to underlie observers' impaired ability to discriminate between separate occurrences of objects with the same identity relative to those with different identities (Kanwisher 1987). Although observers show capacity limits associated with individuating items across both time and space (e.g., Kanwisher 1991; Kanwisher and Potter 1989; Luo and Caramazza 1995, 1996), and previous studies have begun to identify the neural correlates of spatial individuation (e.g., Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007), no study has identified the neural substrates underlying temporal individuation. In the present study we used functional magnetic resonance imaging (fMRI) to investigate the brain regions and mechanisms that are involved in the successful individuation of temporally distinct objects during encoding and how disruptions to this process are represented in the brain.

Initial fMRI investigations into individuation have identified a candidate brain area that might store individuated object representations in visual short-term memory (Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007). Specifically, Xu (2009) found that activity in the inferior intraparietal sulcus (IPS) was sensitive to the number of previously individuated items, regardless of the overall number of perceptual features. This finding suggested that the inferior IPS is involved in storing spatially individuated items and that activity in this region could be dissociated from that in other regions involved in storing object identities. On the basis of their findings, Xu and Chun (2009) proposed the "neural object-file" account, which argues that object individuation is supported by the inferior IPS.

Although Xu and colleagues' investigations suggest a neural basis for spatial individuation, their work focused on a few posterior brain regions and did not explore the contributions of other "higher-level" brain areas. Since recent models of consciousness propose that awareness involves a distributed set of psychological processes and neural substrates (Baars and Franklin 2003; Dehaene et al. 2003; Sergent and Dehaene 2004), individuation could be underpinned by a more diffuse group of regions. In addition, the inferior IPS appears to store individuated representations, yet storage reflects the consequences of individuation rather than the generation of such representations. Here, we are interested in the brain regions that are involved in actively individuating an object during encoding. To address this issue, we directly compared *1*)

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conditions that place high or low demands on temporal individuation processes during encoding and *2*) conditions of successful vs. unsuccessful registration of identical stimuli. To explore the possible role of a more diverse set of regions, our analyses compared changes in blood oxygen level-dependent (BOLD) activity across a wide set of cortical areas.

We employed the repetition blindness (RB) phenomenon to investigate temporal individuation. RB refers to the finding that observers are poorer at reporting two targets embedded in a rapid serial visual presentation (RSVP) if they have the same identity, relative to different identities (Kanwisher 1987; Park and Kanwisher 1994). Kanwisher's (1987) prominent account of RB argues that token information (spatiotemporal properties of an object) for the second target cannot be bound to its type representation (featural and conceptual properties of an object) when it activates the same type as the first target within a short space of time. RB does not reflect a failure to create a type or token for a repeated item, but rather reflects a limitation associated with binding these two representations for conscious report. This deficit is thought to reflect a capacity limit of individuation, because it is strongest when the two targets appear within close temporal or spatial proximity (e.g., Chun 1997; Kanwisher 1987). Kanwisher's account views RB as a perceptual phenomenon, yet other models propose that RB has a later locus, reflecting a retrieval bias or failure (Fagot and Pashler 1995; Whittlesea and Masson 2005). However, because RB has been observed in tasks that have very low memory demands or require immediate responses, there appears to be a significant perceptual component to the effect (e.g., Anderson and Neill 2002; Dux and Marois 2007; Johnston et al. 2002).

We therefore used a RB paradigm to vary the trial-level demands of successfully individuating two sequentially presented stimuli as distinct items by manipulating whether the critical items had the same or different identities. This approach allowed us to investigate two novel questions: First, can temporal individuation be localized to a single brain region (see Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007), or does this process arise from widespread encoding throughout the brain, as suggested by recent models of consciousness (Baars and Franklin 2003; Dehaene et al. 2003; Sergent and Dehaene 2004)? We expected that activity in brain regions involved in temporal individuation would be modulated by the demands placed on this process, whereby it is more demanding to successfully individuate repeated stimuli than nonrepeated stimuli. Second, what neural consequences arise when demands exceed the capacity limit of the individuation process, as reflected by the behavioral RB deficit? We predicted the brain areas that underpin capacity limits that lead to RB would respond differently under conditions where two repeated stimuli were successfully detected compared with when they were not.

MATERIALS AND METHODS

Participants

We recruited 16 volunteers for 2 behavioral experiments ($n = 6$ and 10, respectively; 2 males in each) and 28 volunteers for an fMRI experiment (12 males). The mean ages for participants in the 3 experiments were 26.0 (SD 5.2), 18.8 (SD 1.0), and 23.8 (SD 3.7) yr, respectively. Participants were compensated for their time with course credit or payment. Data from five participants were excluded from the fMRI experiment due to excessive head motion (motion >4 mm/deg in any translational direction or rotation, respectively; henceforth, $n = 23$). All participants had normal or corrected-to-normal vision. Four participants from the first behavioral experiment also participated in the fMRI experiment. The University of Queensland Ethics Committee approved the protocol for all the experiments.

Stimuli

The stimulus set used in all the experiments consisted of 56 indoor and 56 outdoor scenes and scrambled versions of each scene (Marois et al. 2004). All stimuli were presented in grayscale and subtended $11.8° \times 11.8°$ of visual angle at the viewing distance of 57 cm outside the scanner (scene stimuli measured $6.5° \times 6.5°$ of visual angle inside the scanner, viewed from a distance of 90 cm). In the fMRI experiment, we also used 18 photographs of faces from the NimStim face database (Tottenham et al. 2009) for the localizer task. Face stimuli were presented in grayscale and subtended $5.2° \times 6.5°$ of visual angle inside the scanner. Experiments were programmed in MATLAB with the Psychophysics Toolbox (Brainard 1997; Pelli 1997).

Behavioral Experiments

Long intertrial interval RB experiment. We first developed an RB paradigm optimized for fMRI (Fig. 1). This paradigm was based on similar studies that have used pictures or novel objects as stimuli (e.g., Coltheart et al. 2005; Harris and Dux 2005a, 2005b). The purpose of the first behavioral experiment was to assess whether our protocol could elicit the standard RB behavioral effect. Each trial began with a fixation cross for 500 ms, followed by an RSVP stream consisting of a forward scrambled scene mask, three sequentially presented intact scenes (first critical scene, C1; distractor scene; second critical scene, C2), and a backward scrambled scene mask (100 ms/item). We manipulated "scene repetition" within participants such that both critical scenes had either the same identity (repeat) or different identities (nonrepeat). Participants were informed that the distractor scene would never be the same as C1 or C2.

At the end of the RSVP stream, a blank response screen was presented for 3 s, followed by an 8-s intertrial interval (ITI; i.e., a slow event-related fMRI protocol). The participants' task was to report one of three response options during the posttrial 3-s window: They could report that a scene was repeated, no scene was repeated, or only two scenes were presented (catch trial response; see below). Only response accuracy was emphasized. We also ran a behavioral experiment using this RB paradigm without the long ITI (the next trial began immediately after participants made an untimed response), and the pattern of results was comparable to the present experiment (reported below). We chose to use a paradigm in which participants had to detect the presence of a repetition, rather than identify the critical items, because this was more appropriate for studying RB in the scanner with scene stimuli (i.e., responses were forced choice and could be made using a button box). It should be noted that both detection and identification approaches have been used to study RB previously (e.g., Hochhaus and Johnston 1996; Kanwisher et al. 1996; Park and Kanwisher 1994) and are considered to tap the same individuation processes.

As is standard in behavioral investigations of RB, catch trials represented 20% of trials to reduce the likelihood of participants guessing "repeat" on trials where they missed the second repeated scene (Dux and Coltheart 2008; Harris and Dux 2005a, 2005b). These trials only contained two different intact scenes in the RSVP stream. To ensure catch trials lasted for the same duration as repeat and nonrepeat trials (12 s), we included an additional fixation screen for 100 ms between the response window and ITI (see Fig. 1).

Participants were provided with an instruction sheet outlining the task and response keys and completed 20 practice trials before the testing. There were 6 blocks of 25 test trials with an equal number of repeat and nonrepeat trials. The order of the trial types was random.

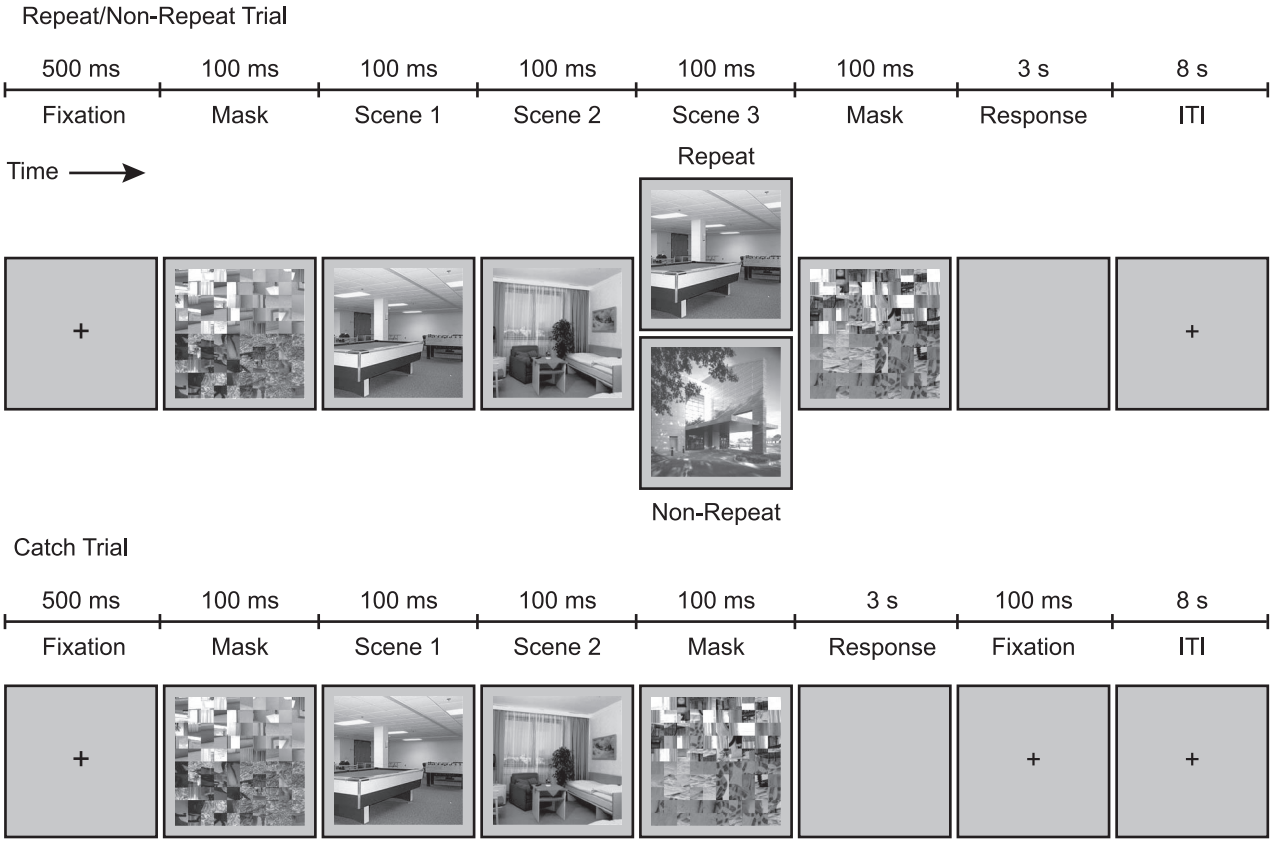

Fig. 1. Schematic representation of the repetition blindness (RB) paradigm. On repeat/nonrepeat trials, participants were presented with a rapid serial visual presentation (RSVP) stream consisting of a forward scrambled scene mask, 3 intact scenes (first critical scene, distractor scene, second critical scene), and a backward scrambled scene mask. The 2 critical scenes were either identical (repeat trial) or different (nonrepeat trial). Only 2 different intact scenes were presented in the RSVP stream on catch trials. Participants reported whether they saw a scene repeated, no scene repeated, or only 2 scenes during the response window. ITI, intertrial interval.

Behavioral experiments were completed on a 20-inch Dell Trinitron CRT monitor with a refresh rate of 100 Hz using a Macintosh mini computer.

Lag RB experiment. We conducted a second behavioral experiment to ensure that our RB paradigm specifically tapped the temporal capacity limits of individuation. The attentional blink (AB) is a similar deficit to RB because it too occurs under dual-target RSVP conditions, is characterized by poorer identification of a second target at short intertarget intervals (e.g., 200–500 ms), and is thought to reflect a failure of perceptual awareness (Chun and Potter 1995; Raymond et al. 1992). The AB, however, occurs under conditions where the two targets have different identities. Thus, in contrast to RB, the AB reflects the temporal capacity limits of object identification, rather than individuation (Chun 1997; see also Dux and Marois 2009). In an additional behavioral experiment, we confirmed that the observed differences in detection accuracy on repeat and nonrepeat trials in the long ITI RB experiment reflected the temporal capacity limits of individuation, rather than identification.

This lag RB experiment was similar to the first behavioral experiment, except we also manipulated the temporal "lag" between C1 and C2 (2, 3, 5, or 7 items). Each RSVP stream consisted of 3 intact scenes (C1, distractor, C2) and 12 scrambled scenes. C1 and the distractor scene always appeared at the sixth and seventh serial positions, respectively. C2 would appear immediately following the distractor scene (*lag 2*) or after one (*lag 3*), three (*lag 5*), or five (*lag 7*) intervening items. The *lag 2* condition had the same temporal gap between C1 and C2 that was used in the long ITI RB experiment and reflects the condition in which the RB deficit is most severe (e.g., Kanwisher 1987; Park and Kanwisher 1994). All scrambled scenes were different. Catch trials were identical to repeat and nonrepeat trials, except C2 was replaced with a scrambled scene, meaning that only two intact scenes were presented. Because this version of the RB paradigm was not used with fMRI, we removed the timed response window and long ITI. Participants responded when prompted at the end of the stream. There were 12 practice trials and 6 blocks of 50 test trials.

fMRI Experiment

In the fMRI experiment, we used the long ITI RB paradigm to manipulate the conditions under which temporal individuation occurred. BOLD activity in response to this task was measured across the whole brain, with a focus on a set of lower- and higher-level a priori regions of interest (ROIs; see below). This paradigm included 200 trials split over 8 event-related runs, with 80 repeat, 80 nonrepeat, and 40 catch trials. Each run consisted of a 20-s fixation period followed by 25 RB trials and then a 12-s fixation period. Participants responded by pressing one of two buttons on a button box in their right hand for repeat and nonrepeat responses or one button with their left hand for catch responses. The order of trial types was random, and the number of trials for each condition was equal across runs.

Localizer task. After the RB runs, participants completed the localizer task. Participants were presented with separate 20-s blocks of fixation, face, and scene stimuli. At the beginning of each stimulus block, a visual cue was presented for 2 s to indicate the block type. Each block included nine trials in which an intact scene or face was presented for 1 s, followed by a 1-s ITI. On half the scene and face blocks, participants were cued to passively view the stimuli ("passive scene" and "passive face"). On the remaining blocks, participants were cued to classify the scenes as indoor or outdoor scenes ("task

scene") or the faces as male or female ("task face"). This response was speeded and was made using one of two buttons on a response box in the left or right hand, respectively.

There were two localizer runs where each consisted of four blocks of fixation and three blocks of each of the stimulus block types. The order of the stimulus blocks was random without replacement, and a fixation block was presented after every four stimulus blocks. An additional 8-s fixation period was presented at the start and end of each localizer run.

Data acquisition. Images were acquired using a 3T Siemens Trio MRI scanner (Erlangen, Germany). Participants lay supine in the scanner and viewed the visual display via rear projection onto a mirror mounted on a 12-channel head coil. A T1-weighted anatomic image was collected in the middle of the scanning session using an MPRAGE sequence [repetition time (TR) = 1.9 s, echo time (TE) = 2.32 ms, flip angle (FA) = 9°, field of view (FOV) = 192 × 230 × 256, resolution = 1 mm^3]. Functional T2*-weighted images were acquired parallel to the anterior commissure-posterior commissure plane using a GRE EPI sequence (TR = 2 s, TE = 25 ms, FA = 90°, FOV = 192 × 192, matrix = 64 × 64, in-plane resolution = 3 × 3 mm). Each volume consisted of 33 slices (thickness = 3 mm, interslice gap = 0.3 mm), providing whole brain coverage. We synchronized the stimulus presentation with the acquisition of functional volumes. There were 166 and 168 volumes (including 4 dummy volumes) acquired for each of the event-related and localizer runs, respectively.

Data analyses. We analyzed our data using Brain Voyager QX software (Brain Innovation, Maastricht, The Netherlands) and custom MATLAB code.

PREPROCESSING. Data preprocessing included three-dimensional (3-D) motion correction (where each functional image was aligned to the first run), slice-scan time correction, and high-pass temporal filtering (3 cycles per run). All functional images were coregistered to the anatomic scan and transformed into standardized space (Talairach and Tourmoux 1988). No spatial smoothing was applied to preserve fine-grained spatial information for the multivoxel pattern analyses (MVPA; see below).

REGIONS OF INTEREST. We first isolated a group of 20 ROIs (Table 1). These regions consisted of perceptual areas involved in processing scenes (parahippocampal place area, PPA; Epstein et al. 2003) and objects (lateral occipital complex, LOC; Kourtzi and Kanwisher 2001), regions previously implicated in object individuation and identification (see Xu 2009), and higher-level attentional/executive areas associated with capacity limits of information processing (Dux et al. 2006, 2009; Heekeren et al. 2004; Jiang and Kanwisher 2003; Marois et al. 2006; Schubert and Szameitat 2003; Szameitat et al. 2002). Given the extensive overlap between the superior parietal lobule and superior IPS ROIs in the majority of subjects, we collapsed univariate and multivariate results across these two parietal regions (denoted as sIPS/SPL); hence, 18 ROIs were examined.

To localize these ROIs in each participant, we submitted data from the localizer runs to single-participant general linear model voxelwise analyses using a statistical threshold of $q < 0.05$ (false discovery rate, FDR). We defined regressors for the fixation, passive face, task face, passive scene and task scene blocks, which were then convolved with a double-gamma hemodynamic response function. To isolate the PPA, we contrasted activity between scene and face blocks. Bilateral PPA ROIs were identified as active voxels in the anterior section of the parahippocampal gyrus in the left and right hemisphere (Epstein et al. 2003). To isolate the remaining ROIs, we contrasted activity in the four stimulus blocks with fixation. We defined the object perception and attentional/executive ROIs on these statistical maps using mean Talairach coordinates derived from Xu (2009) and Dux et al. (2009), respectively, as a guide for establishing the most relevant functionally defined regions. Each ROI was identified as the cluster of active voxels that most closely matched the previously established coordinates for that region. If there were two noncontiguous equidistant activation clusters, we used whichever cluster was still present at a more stringent threshold. In each region, we only analyzed data from the event-related runs for participants in which that ROI could be isolated (see Table 1).

Table 1. *Anatomic locations of the ROIs*

ROI	No. of Participants	Talairach Coordinates (*x*, *y*, *z*)
Attentional/executive		
IFJ (L)	18	−43 (2.4), 8 (2.6), 29 (3.1)
IFJ (R)	20	44 (5.0), 8 (2.9), 28 (2.4)
ACC (Bi)	22	1 (6.7), 11 (3.7), 39 (2.9)
SMFC (Bi)	23	−2 (4.2), −3 (4.1), 57 (2.4)
DLPFC (L)	19	−33 (3.7), 31 (6.1), 29 (4.8)
DLPFC (R)	15	37 (5.1), 30 (2.6), 28 (4.6)
PMC (L)	21	−27 (3.9), −8 (3.2), 50 (4.9)
PMC (R)	21	30 (4.4), −6 (4.1), 48 (3.6)
SPL (L)	21	−27 (2.8), −56 (3.6), 44 (3.1)
SPL (R)	21	26 (3.0), −58 (3.8), 45 (3.1)
Insula (L)	19	−33 (4.3), 16 (5.3), 10 (4.0)
Insula (R)	19	34 (4.4), 18 (4.6), 8 (4.0)
Object perception		
Inferior IPS (L)	22	−28 (4.1), −78 (6.2), 25 (4.7)
Inferior IPS (R)	22	27 (4.0), −77 (3.7), 25 (4.0)
Superior IPS (L)	23	−26 (3.7), −62 (2.8), 40 (3.8)
Superior IPS (R)	23	26 (3.7), −56 (4.9), 44 (3.1)
LOC (L)	23	−34 (3.2), −80 (3.4), 13 (3.1)
LOC (R)	22	46 (3.9), −59 (4.2), 4 (4.4)
Scene perception		
PPA (L)	23	−24 (2.1), −42 (2.3), −6 (1.7)
PPA (R)	23	24 (1.9), −42 (1.7), −6 (1.6)

All regions were isolated using data from the localizer task. Attentional/executive and object perception ROIs were isolated by contrasting activity between stimuli blocks with fixation. The scene perception ROIs were localized by contrasting activity between scene and face stimuli blocks. No. of participants data indicates the number of participants for whom an ROI was successfully identified. Talairach coordinates (*x*, *y*, *z*) represent the mean Talairach for each brain region with SD in parentheses. IFJ, inferior frontal junction; ACC, anterior cingulate cortex; SMFC, superior medial frontal cortex; DLPFC, dorsal lateral prefrontal cortex; PMC, premotor cortex; SPL, superior parietal lobule; sIPS, superior intra-parietal sulcus; iIPS, inferior intraparietal sulcus; LOC, lateral occipital complex; PPA, parahippocampal place area. L, left; R, right; Bi, bilateral.

For the univariate analysis, an ROI included all voxels above statistical threshold surrounding the peak voxel up to a maximum of 6 × 6 × 6 mm (8 voxels). For the multivariate analysis, ROIs were defined by a 15 × 15 × 15-mm and 21 × 21 × 21-mm cube (125 and 343 voxels, respectively), centered on each individual participant's Talairach coordinates of the peak voxel. We used larger ROI sizes in the multivariate analysis to increase variance across voxels and to be consistent with other studies that have employed this analytic technique (e.g., Gallivan et al. 2011; Harrison and Tong 2009; Kamitani and Tong 2005; Oosterhof et al. 2012). We defined ROIs for the multivariate analyses using two different sizes to ensure that decoding results were reliable, regardless of the particular number of voxels included in the analysis (Spiridon and Kanwisher 2002). We only report the MVPA results for ROIs defined by a 21 × 21 × 21-mm cube, but our findings were consistent across both ROI sizes unless otherwise stated.

UNIVARIATE ANALYSIS. We first analyzed data from the RB event-related runs using a standard univariate approach. Time courses for each condition, ROI (with signal averaged across all voxels in the ROI), and participant were extracted. Percent signal change was calculated relative to signal during the volume preceding trial onset. This baseline was chosen to exclude any potential activity associated with the previous trial. Individual participant time courses were averaged across all participants, and we compared differences in peak amplitude between the experimental conditions. Peak amplitude was

defined as the averaged signal across time points 4–8 s post-trial onset. Statistical significance was assessed using repeated-measures *t*-tests and a statistical threshold of $P < 0.05$ (Bonferroni corrected for the 18 regions tested).

MULTIVARIATE ANALYSES. To increase the sensitivity of our analysis, we also analyzed our data using MVPA (Haynes and Rees 2006; Kamitani and Tong 2005). This analytic approach is more sensitive than univariate methods because it examines differences in activity across multiple voxels, rather than each voxel individually. Indeed, activity within any single voxel might show weak differences between conditions if only a small proportion of neurons in that voxel code for information associated with the experimental task. MVPA attempts to improve the sensitivity of fMRI analysis by pooling these weak, but reliable, signals across voxels and comparing conditions based on the resulting ensemble patterns of activity. MVPA was implemented using custom MATLAB software and a linear support vector machine binary algorithm (Chang and Lin 2011).

For each voxel in a given ROI, we extracted the average percent signal change corresponding to the peak of the time course for each trial (4–8 s post-trial onset). Before each MVPA, data for each voxel in an ROI were *z*-transformed and mean-centered by subtracting the condition mean for the entire ROI from the response in each individual voxel to control for overall differences in signal amplitude between conditions (see Esterman et al. 2009; Tamber-Rosenau et al. 2011). We trained a series of binary classifiers to discriminate between patterns of activity associated with the experimental conditions using the leave-one-out cross-validation method. In each fold, one run was used to test the classifier's generalization performance and the remaining seven runs were used to train the classifier. Decoding accuracy for each ROI was averaged across each cross-validation loop and tested against chance accuracy (50%) using one-sample *t*-tests and a statistical threshold of $P < 0.05$ (Bonferroni corrected for the 18 regions tested). If there is a functional distinction between pools of neurons within a given ROI that respond to each condition, then the classifier should be better than chance at discriminating between patterns of activity on the test trials (Pereira et al. 2009).

We also performed a searchlight analysis to explore whether other regions outside our ROIs showed a similar pattern of results to the ROIs we tested (Kriegeskorte et al. 2006). A spherical searchlight ROI with a 2-voxel radius (33 voxels) was centered on every voxel of the volume. We used the same cross-validation classification method procedure as the ROI analysis to test for information contained in these local activity patterns. Classification accuracy for each searchlight was assigned to the central voxel and compared against chance performance to test for significance ($q < 0.05$, FDR).

RESULTS

All statistical analyses were conducted with a two-tailed alpha level of 0.05, and Bonferroni correction was applied for multiple comparisons unless otherwise stated.

Behavioral Experiments

Chance performance in the RB task was 33.3%. To first assess whether our paradigm could elicit the standard RB behavioral effect, we submitted the mean detection accuracy data from the long ITI RB experiment to a repeated-measures *t*-test. Detection accuracy reflects the percentage of trials in which participants correctly detected the identity of the two critical scenes (e.g., a "repeat" response on repeat trials; "nonrepeat" or "2 scene only" responses would be considered incorrect on this trial). Consistent with other RB studies that have used a paradigm similar to ours (e.g., Hochhaus and Johnston 1996; Kanwisher et al. 1996; Park and Kanwisher 1994), participants were significantly less accurate on repeat trials relative to nonrepeat trials: $t(5) = 2.93$, $P = 0.033$ (see Fig. 2*A*). In subsequent experiments conducted in our laboratory, we have replicated this RB result using alphanumeric stimuli, suggesting that this behavioral effect is not specific to the type of stimulus used. Performance on catch trials was around chance in this experiment [mean 36.7%, SD 8.2%; $t(5) < 1$], where participants' erroneous responses were more likely to be a nonrepeat response than a repeat response (69.6 vs. 25.2% of errors, respectively; the remaining 5.2% of errors were absent responses). This proportion and pattern of catch trial errors are consistent with previous RB studies (Dux and Coltheart 2008).

Data from the lag RB experiment were used to test whether our RB paradigm specifically tapped the temporal capacity limits of individuation, rather than identification. If our paradigm elicited identification limitations, we expected participants would be poorer at detecting both repeated and nonrepeated scenes at shorter temporal lags, relative to longer temporal lags. On the other hand, deficits in individuation indicate a specific difficulty in registering two repeated items as separate items. Thus, if our paradigm only tapped the temporal capacity limits of individuation, we predicted detection of repeated scenes alone would be affected by lag.

To assess this, we submitted mean detection accuracy data from the lag RB experiment to a 2 (scene repetition: repeat, nonrepeat) by 4 (lag: 2, 3, 5, 7) repeated-measures ANOVA. A

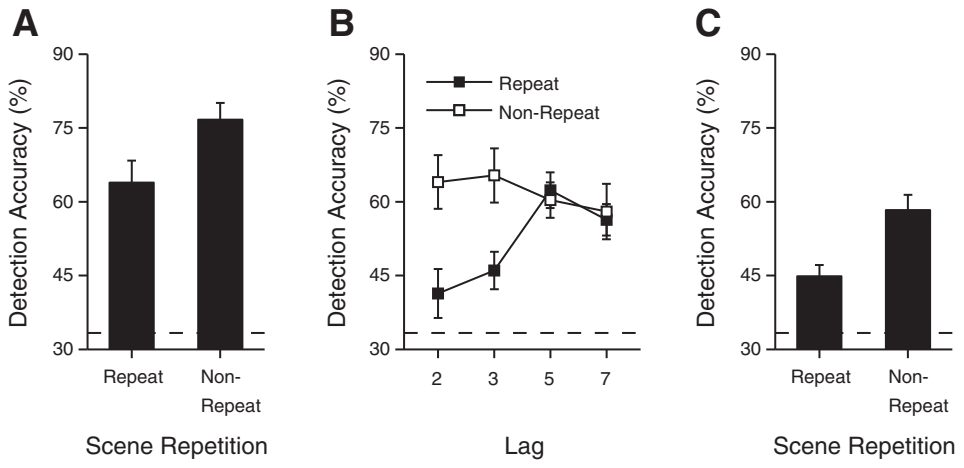

Fig. 2. Behavioral results from the behavioral and functional MRI (fMRI) experiments. *A*: mean detection accuracy results from the long ITI RB experiment, separately for repeat and nonrepeat trials. *B*: mean detection accuracy from the lag RB experiment, separately for repeat and nonrepeat trials across the 4 temporal lag conditions. *C*: mean detection accuracy results from the fMRI experiment, separately for repeat and nonrepeat trials. Error bars represent SE of the mean across participants, and the dashed line indicates chance performance (33.3%).

Table 2. *Average response proportions to repeat, nonrepeat, and catch trials in the fMRI experiment*

	Response				
Trial Type	Repeated	Nonrepeated	Catch	Absent	Total
Repeat	0.45 (0.11)	0.25 (0.10)	0.05 (0.04)	0.26 (0.13)	1.00
Nonrepeat	0.14 (0.14)	0.58 (0.15)	0.10 (0.08)	0.18 (0.11)	1.00
Catch	0.11 (0.09)	0.28 (0.13)	0.46 (0.23)	0.15 (0.10)	1.00

Values are means (SD).

significant main effect was found for both scene repetition [$F(1, 9) = 5.51$, mean squared error (MSE) = 394, $P = 0.044$, $\eta_p^2 = 0.38$] and lag [$F(3, 27) = 4.44$, MSE = 75, $P = 0.012$, $\eta_p^2 = 0.33$] (see Fig. 2*B*). Crucially, a significant interaction between these two factors also emerged [$F(3, 27) = 6.28$, MSE = 169, $P = 0.002$, $\eta_p^2 = 0.41$]. Follow-up *t*-tests revealed detection accuracy on repeat trials was significantly reduced at shorter lags (*lags 2* and *3*) relative to longer lags (*lags 5* and *7*) [$t(9) = 5.55$, $P < 0.001$], but detection accuracy on nonrepeat trials did not vary with lag [$t(9) = 1.31$, $P = 0.222$]. Thus our RB paradigm specifically tapped temporal capacity limitations associated with individuation, rather than identification. These findings demonstrate that the present paradigm elicited a pure RB effect that was not confounded by the AB. Similar to the first behavioral experiment, catch trial performance was no greater than chance [mean 24.5%, SD 16.2%; $t(9) = 1.72$, $P = 0.119$].

fMRI Experiment

Behavioral performance. A repeated-measures *t*-test revealed that behavioral performance on the RB task inside the scanner was consistent with previous behavioral experiments, whereby detection accuracy was reduced on repeat trials relative to nonrepeat trials [$t(22) = 4.72$, $P < 0.001$; see Fig. 2*C*]. In contrast to the behavioral experiments, however, performance on catch trials was significantly above chance [mean 46.4%, SD 5.0%; $t(22) = 2.67$, $P = 0.014$], with participants more likely to make erroneous nonrepeat than repeat responses (54.0 vs. 27.1% of errors, respectively; the remaining 19.0% of errors were absent responses). Participants could successfully complete the task blocks on the localizer runs as behavioral performance was close to ceiling (means >93.0%, SDs < 1.2%; *t*s >36.06, *P*s <0.001 compared with chance).

Trial types and comparisons. For the fMRI analyses, we binned repeat and nonrepeat trials into the following conditions: hit (repeat trial, repeat response), miss (repeat trial, nonrepeat response), correct rejection (nonrepeat trial, nonrepeat response), and false alarm (nonrepeat trial, repeat response). Table 2 displays the average response proportions for all conditions. Note that catch trials (or repeat/nonrepeat trials where a "2 scene only" response or no response was made) were not included in the fMRI analyses because these trials served only as filler trials to reduce the likelihood of guessing responses.

To first isolate the brain areas involved in temporally individuating items during encoding, we compared hit and correct rejection trials, because these conditions place different demands on individuation. That is, given that repeated stimuli presented in close temporal proximity are more difficult to individuate relative to nonrepeated stimuli (Kanwisher 1987), hit trials should, on average, place greater demands on the process of temporal individuation, relative to correct rejection trials. It is important to note that this comparison reflects only trials on which a correct response was made, and we therefore know, with some degree of certainty, that the scenes were successfully individuated in both trial types (although this process was more demanding in under hit trials). In addition, this comparison is balanced in terms of reward associated with making a correct response.

Our second key comparison aimed to identify brain areas involved in the RB deficit (i.e., regions that may underlie the capacity limit on temporal individuation). To do this, we contrasted hit and miss trials, because this comparison reflects instances where two repeated stimuli are successfully detected or not. Because RB reflects an inability to bind a second repeated item's identity to its token, rather than a failure to create the second token altogether (Kanwisher 1987; Kanwisher et al. 1995; Park and Kanwisher 1994), it was more appropriate to compare between conditions that reflect a misidentification error, rather than trials where participants reported seeing nothing at all (e.g., hits vs. repeated scene/"2 scene only" response trials). Even though this RB comparison uses trial definitions that are based on a postrun selection of trials by accuracy, this is a common approach employed in imaging studies that use RSVP tasks (e.g., Marois et al. 2004). We tested for differences using both univariate gross amplitude and multivariate spatial patterns of BOLD activity.

Univariate analyses. For the demands on temporal individuation comparison, we found no significant amplitude differences between hit and correct rejection trials. This finding suggests that the amplitude of activity in all of our ROIs was not modulated by conditions that place differential demands on temporal individuation. On the other hand, when we compared between conditions that reflect a capacity limit of temporal individuation, we found a single region (left hemisphere premotor cortex) that showed significantly greater activity on miss trials relative to hit trials [$t(20) = 3.42$, $P = 0.049$, corrected for multiple comparisons; see Fig. 3]. Thus processing in this region may be involved in RB.

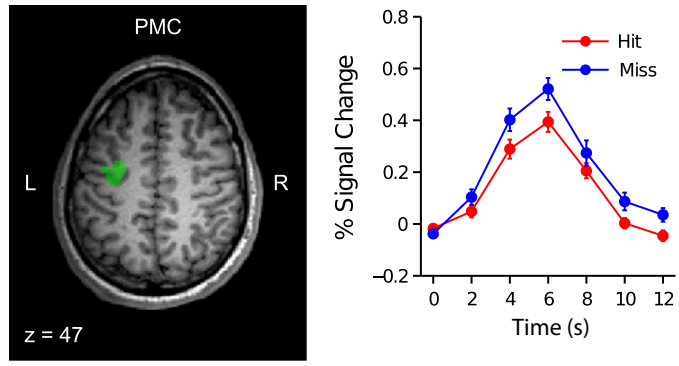

Fig. 3. *Left*: the single significant region of interest (ROI) that reflected changes in gross blood oxygen level-dependent (BOLD) amplitude for the capacity limits of temporal individuation. Anatomic image shows individual ROIs from all participants for whom an ROI could be identified for that given area. L, left hemisphere; R, right hemisphere; PMC, premotor cortex. *Right*: because none of the ROIs showed significant differences in BOLD amplitude between hit and correct rejection trials (demands on temporal individuation comparison), the graph only displays the BOLD time course for hit and miss trials for this region. Error bars denote SE of the mean across participants. Peak amplitude was taken as the average signal across volumes 4–8 s post-trial onset.

These gross differences in BOLD amplitude were specific to the successful individuation of two repeated stimuli, because none of our ROIs showed any differences in amplitude between correct and incorrect nonrepeated trials (correct rejections vs. false alarms; ts < 2.16, corrected for multiple comparisons Ps > 0.809). This result is consistent with behavioral findings from the lag RB experiment in that it shows that our paradigm specifically taps processing limitations associated with the perception of two repeated stimuli, but not two nonrepeated stimuli (see also Chun 1997). In addition, this difference in amplitude cannot simply reflect response conflict or ambiguity, because this same region responded similarly on hit and false alarm trials ($t < 1$). These trial types showed the greatest difference in reaction time (1,166 vs. 1,430 ms; although response speed was not emphasized in the task) and would arguably reflect the greatest difference in response uncertainty.

Multivariate analyses. We further explored the neural underpinnings of temporal individuation and its capacity limits by using ROI-based and whole brain searchlight MVPAs. Because our experimental conditions were jointly determined by stimulus presentation and participants' responses, the number of trials in each condition was not balanced. Unbalanced trials are particularly problematic for MVPA because this can bias the classifier toward the more numerous condition, rather than the actual properties associated with the experimental conditions (Pereira et al. 2009). To address this issue, we balanced trial numbers across conditions in both training and testing subsets by removing a random selection of trials from the more plentiful condition before the MVPA. Decoding results for the ROI-based MVPA were averaged across 100 repetitions of this procedure, and the number of iterations was reduced to 10 for the searchlight analysis to save computation time. With the use of this strict balancing method, there was an average of 35 trials in training sets and 5 trials in testing sets in each cross-validation loop.

ROI-based MVPA. To first identify differences in activity patterns associated with the demands placed on temporal individuation, we trained a classifier to discriminate between hit and correct rejection trials in each of our ROIs. Above-chance decoding performance for this comparison emerged in 17 of our 18 ROIs (ts > 4.22, Ps < 0.010, corrected for multiple comparisons; see Fig. 4). Although activity in the left hemisphere dorsolateral prefrontal cortex (DLPFC) could be discriminated between these two conditions for the 21-mm ROI cube, this result did not hold for the 15-mm ROI cube [$t(18) = 2.28$, $P = 0.637$]. The significant ROIs included both lower-level areas involved in perceptual processes (e.g., Epstein et al. 2003; Kourtzi and Kanwisher 2001; Xu 2009) and higher-level executive areas that have previously been associated with other capacity-limited processes, such as response selection, decision making, and encoding (e.g., Dux et al. 2006, 2009; Heekeren et al. 2004; Szameitat et al. 2002; Tombu et al. 2011). In contrast, the classifier was only able to differentiate between activity patterns associated with successful and unsuccessful instances of temporal individuation (hits vs. misses) in the left hemisphere superior IPS/SPL [$t(21) = 3.58$, $P = 0.031$, corrected for multiple comparisons]. This result, however, did not hold over changes in ROI size (classification under 15-mm ROI cube, corrected for multiple comparisons $P > 1$). These multivariate results therefore suggest that perceptual demands placed on temporal individuation influence the patterns of activity across a widely distributed set of brain regions, including both lower and higher cortical areas. This finding contrasts with the single brain region that has previously been associated with spatial individuation (Xu 2009) in that it suggests that this process is underpinned by a far more distributed set of areas. The processing limitations associated with individuation, however, have no consistent effect on the ensemble patterns of activity in any region.

Control analyses. We conducted an additional set of control MVPAs to test whether the distributed differences in activity patterns associated with hit and correct rejection trials were driven by other differences that existed between these conditions (i.e., not related to individuation). Because hit and correct rejection trials showed significant differences in reaction time [1,166 vs. 1,297 ms; $t(22) = 4.23$, $P < 0.001$], the first control analysis aimed to assess whether our results could be attributed to task-related effects such as general difficulty or the amount of time spent on the task. Using reaction time as a proxy for task difficulty, we trained classifiers to discriminate between the two trial types that showed the largest difference in reaction time: hit (1,166 ms) and false alarm (1,430 ms) trials [$t(22) = 5.50$, $P < 0.001$]. Significant decoding emerged for this comparison in the anterior cingulate cortex (ACC) and right hemisphere LOC (ts > 3.46, Ps < 0.042, corrected for multiple comparisons); however, only the ACC result was also observed for the 15-mm cube [ACC: $t(21) = 3.94$, $P = 0.014$; right hemisphere LOC: $t(21) = 2.96$, $P = 0.134$]. Results from this control analysis suggest that, with the possible exception of the ACC, the distributed patterns of activity associated with the perceptual demands placed on temporal individuation do not simply reflect task difficulty or the amount of time spent on the task. In contrast to the remaining ROIs, the activity patterns in the ACC likely reflect general task difficulty as opposed to a specific difficulty associated with individuating two scenes. Furthermore, the lack of significant results are unlikely to reflect insufficient power due to the low number of false alarm trials, because our results from the demands on temporal individuation comparison held for all previously significant ROIs (ts > 3.29, $P = 0.078$ for left hemisphere inferior frontal junction; ts > 3.48, Ps < 0.048 for all other ROIs, both corrected for multiple comparisons) even when we equated trial numbers across all trial types, rather than only across the conditions being compared.

The second set of control analyses tested whether the differences in activity patterns associated with temporal individuation reflected purely stimulus- or response-related effects, since hit and correct rejection conditions differed on both these factors. To first test for stimulus-related differences in activity, we decoded patterns of activity associated with repeated and nonrepeated stimuli, regardless of participants' responses. For this analysis, we collapsed across both repeated stimulus (hits and misses) and nonrepeated stimulus conditions (correct rejections and false alarms) to give ourselves the best chance of detecting any stimulus-related effects if they did indeed exist. Because we used all four trial types in this analysis, we balanced trial numbers across all conditions before decoding to ensure the differences in trial numbers did not affect the results. No significant decoding emerged between repeated and nonrepeated stimulus conditions in any region [ts < 2.97, Ps > 0.126, corrected for multiple comparisons; see Fig. 5], suggest-

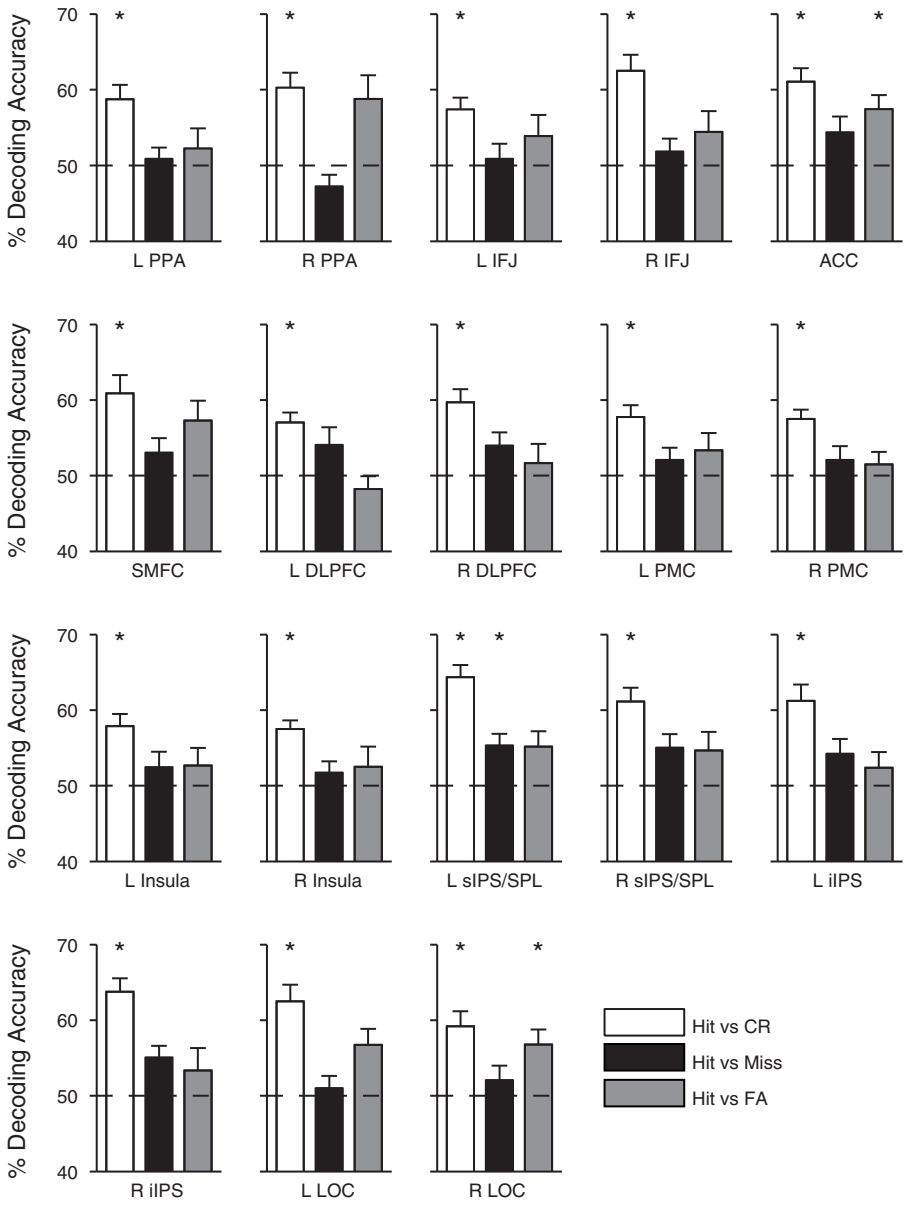

Fig. 4. Results from the main multivariate analyses and task difficulty control analysis. The hit vs. correct rejection (CR) comparison reflects differences in the demands placed on temporal individuation (open bars). The hit vs. miss comparison identifies the neural consequences associated with the capacity limits of temporal individuation (solid bars). The hit vs. false alarm (FA) comparison reflect reaction time differences as a proxy for task difficulty-related changes in activity patterns (shaded bars). Chance performance is indicated by the dashed lines. $*P < 0.05$ reflects greater than chance performance (corrected for multiple comparisons). Error bars represent SE of the mean. Region abbreviations are as defined in Table 1.

ing that none of our ROIs exclusively coded for stimulus properties in this experiment.

We also decoded activity patterns associated with repeated and nonrepeated responses regardless of the stimulus presentation (hits and false alarms vs. misses and correct rejections) and found these two conditions could be discriminated in 2 of the 18 ROIs: the right hemisphere PPA and left hemisphere sIPS/SPL (ts > 3.38, Ps < 0.048, corrected; see Fig. 5). The same decoding performance in these regions did not hold across both ROI sizes, however, suggesting that the response coding in these regions was not reliable (ts < 2.80, Ps > 0.189 for 15-mm ROI cube). Thus the widespread differences in patterns of activity associated with hit and correct rejection conditions did not appear to be purely stimulus or response based, but rather reflected an interaction between these stimulus and decision/response factors that would be necessary to individuate temporally distinct items.

Although our results were not driven by stimulus and response factors individually, one could argue that they reflect a simple stimulus-response interaction, rather than anything specific to temporal individuation. To provide further support that our hit vs. correct rejection comparison reflects temporal individuation demands, rather than some other sort of stimulus-response interaction, we decoded miss vs. false alarm trials (we balanced trial numbers in this comparison as well, like all other analyses). These are both incorrect trials, so we cannot be sure of the extent to which each critical item was individuated, but these trials do differ in terms of the stimulus presented and the response made. Unlike our key analysis of hit vs. correct rejection, the analysis of miss vs. false alarm revealed significant decoding in the bilateral LOC only (ts > 3.49, Ps $< .039$, corrected). Importantly, after averaging over decoding values in all the ROIs, to increase statistical power and counter the fact that not all subjects showed every ROI (see Table 1), we found that the overall decoding across the brain for hits vs. correct rejections was significantly greater than that found for misses vs. false alarms [$t(22) = 2.91$, $P = 0.008$, uncorrected because data were averaged across all ROIs]. Collectively,

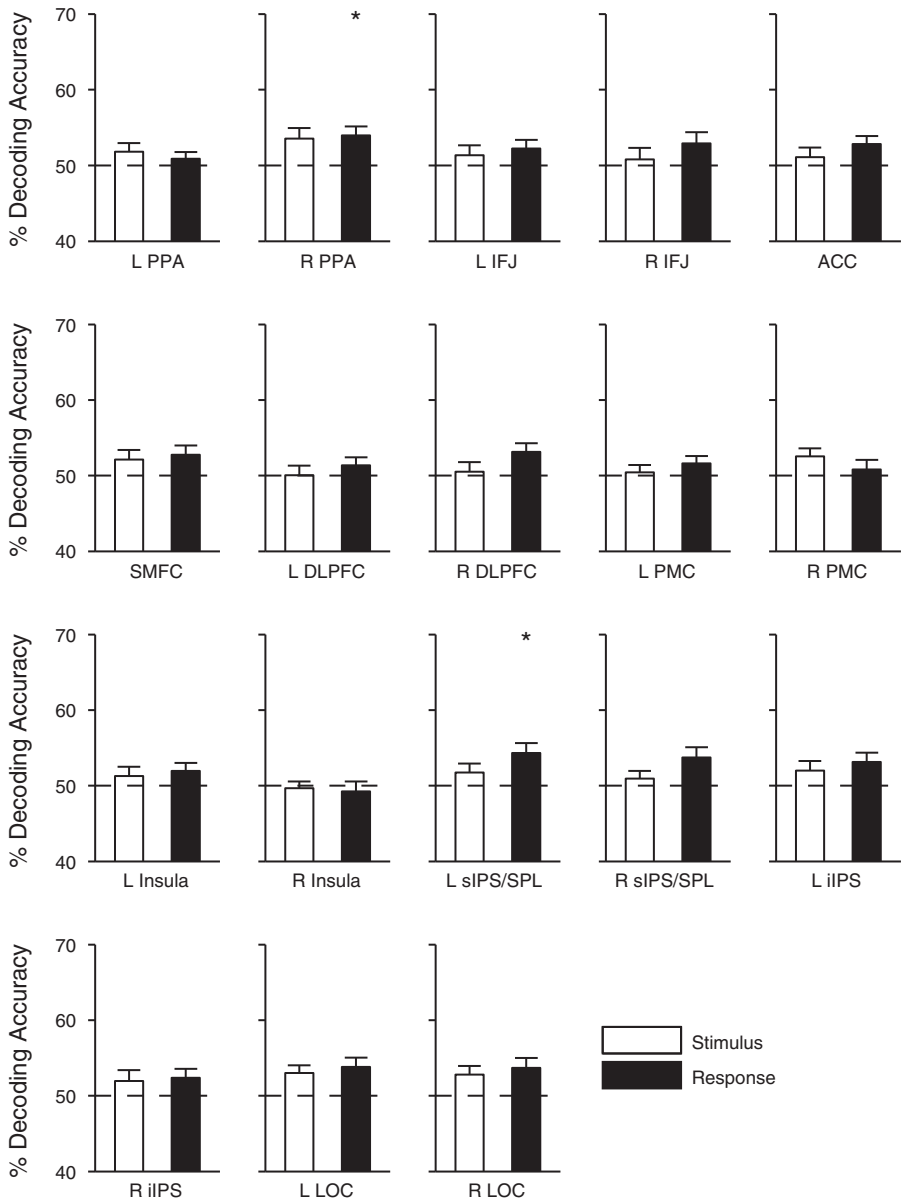

Fig. 5. Results from the stimulus and response multivariate control analyses. Format is the same as Fig. 4. To identify purely stimulus-driven changes in activity patterns, we compared repeated and nonrepeated stimuli trials, regardless of participants' responses (hit and miss vs. CR and FA; open bars). Likewise, to isolate purely response-driven changes in activity patterns, we contrasted instances where participants made a repeated and nonrepeated response, regardless of the stimulus presentation (hit and FA vs. CR and miss; solid bars).

these results suggest all significant hit vs. correct rejection ROIs, with the possible exception of the bilateral LOC, reflect the specific stimulus-response interaction involved in temporal individuation. As we elaborate on in the DISCUSSION, we propose that such interactions are facilitated within a distributed neural framework or "workspace" in which information can be shared between lower and higher regions (Baars and Franklin 2003; Dehaene et al. 2003; Sergent and Dehaene 2004).

A final control analysis was conducted to ensure that results from the demands on temporal individuation analysis did not simply reflect a data artifact that would produce above chance decoding across the entire brain. To test this, we decoded activity patterns in two additional control ROIs that predominantly respond to auditory information rather than visual information (left and right primary auditory cortices). These ROIs were anatomically defined as the superior region of the temporal lobe (Rademacher et al. 2001). We decoded activity in these areas for the two main comparisons and the task difficulty control comparison. If decoding performance in the temporal individuation analysis did indeed reflect the differential perceptual demands associated with individuating visual stimuli across time (and not an artifact in the data, task design, or analysis), the classifier should be no better than chance at discriminating between hit and correct rejection conditions in either of these control regions. Consistent with this prediction, no significant decoding emerged in either of the auditory ROIs for any of the classifier comparisons, including the demands on temporal individuation comparison (ts < 2.32, Ps > 0.544, corrected for multiple comparisons; Fig. 6).

Searchlight analysis. We conducted a whole brain searchlight analysis to determine if brain regions other than our ROIs could discriminate between the different demands placed on temporal individuation. Consistent with our previous ROI-based MVPA, the searchlight analysis revealed that widespread parts of the brain show distinct activity patterns for hit compared with correct rejection trials (Fig. 7). The information map generated from this analysis included all of our ROIs and provided confirmatory support for the findings that emerged in

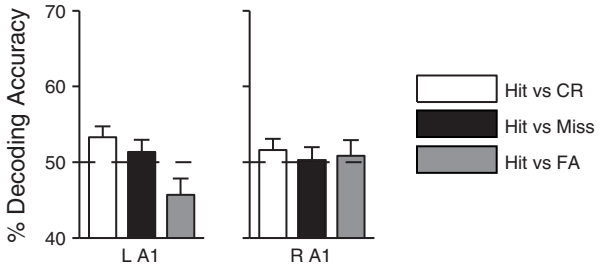

Fig. 6. Results for the main multivariate analyses and task difficulty control multivariate analysis for the 2 control regions. Format is the same as Fig. 4 and reflects the same comparisons. A1, primary auditory cortex.

our ROI-based MVPA. In addition to these ROIs, we also found that large parts of the frontal, parietal, and occipital cortices were sensitive to the conditions under which temporal individuation occurred. Consistent with our control ROI analysis, no voxels in the auditory cortices could be reliably classified, suggesting that our classification results do not reflect an artifact of the data analyses. We also performed a searchlight analysis for the RB comparison but found no significant classification across the entire brain. This finding further supports the idea that the processing limitations that lead to RB modulate the amplitude, rather than the patterns, of BOLD activity.

DISCUSSION

The purpose of the present study was twofold. First, we aimed to examine whether individuation processes could be localized to a single neural correlate or if this operation tapped a widely distributed network of brain areas, as has been proposed in models of consciousness and encoding (Baars and Franklin 2003; Dehaene et al. 2003; Sergent and Dehaene 2004). Second, we aimed to pinpoint the neural areas involved in the behavioral RB deficit. To accomplish these goals, we employed an RB paradigm and a combination of univariate and multivariate analysis techniques. In response to the first aim, we found that activity patterns associated with the perception of two repeated stimuli (which are more demanding to individuate) and nonrepeated stimuli (which are relatively easy to individuate) could be successfully discriminated. Critically, these two conditions reflected correct trials, meaning that we can be confident that stimuli were successfully individuated on these trials, although this process was more demanding for repeated stimuli. Even though these two conditions could not be distinguished when univariate BOLD amplitude was compared, our multivariate analyses revealed that these conditions elicited reliably different spatial patterns of activity in the majority of our ROIs. This set of regions included both lower-level perceptual and higher-level attentional/executive regions that covered parts of the frontal, parietal, and occipital cortices. Although we cannot be sure of the stage(s) of processing at which the increased demands associated with temporal individuation had their impact, our findings nevertheless demonstrate a measurable difference in BOLD activity that is evoked by these changes in temporal individuation demands.

For our secondary analysis, to identify the brain area(s) associated with RB (i.e., a processing limitation associated with temporal individuation), we compared activity between conditions in which two repeated stimuli were successfully detected or not. In contrast to the primary analysis in which we manipulated the demands on temporal individuation, we found that this RB analysis did not reliably affect the spatial patterns of activity in any of our ROIs, but instead modulated the amplitude of BOLD activity in the left hemisphere premotor cortex. Together, our findings suggest that a large group of

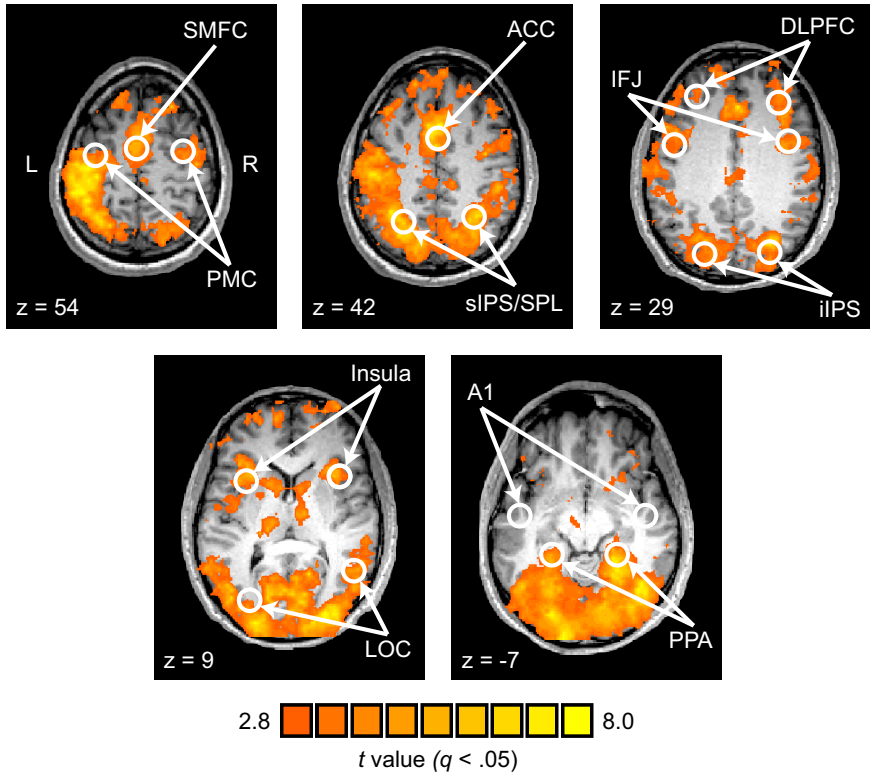

Fig. 7. Results for the whole brain searchlight analysis for the demands on temporal individuation comparison. We centered a searchlight ROI (33 voxels) on every voxel in the volume and tested for differences in these local patterns for hits vs. CRs. Classification accuracies were compared with chance performance (50%), and t values are only displayed for voxels that survived the multiple comparisons correction ($q < 0.05$). Region abbreviations are as defined in Table 1.

cortical regions are sensitive to demands placed on the temporal individuation process, whereas the processing limitations associated with this operation that lead to RB specifically influence the strength of activity in a focal brain region. Our two key comparisons therefore appear to reflect distinct processes: the demand or load associated with constructing an individuated representation across time, and a specific capacity limitation associated with individuation.

The differences that emerged for the amplitude and patterns of BOLD activity resonate with recent findings in the visual short-term memory literature. Several studies have shown that increasing the number of items held in memory leads to sustained, elevated BOLD amplitude in the parietal cortex (Todd and Marois 2004; Xu and Chun 2006), yet maintaining these items in memory alters the patterns, but not the amplitude, of activity in early sensory areas (e.g., Emrich et al. 2013; Serences et al. 2009). Emrich et al. (2013) suggest that changes in activity patterns in sensory areas reflect the precision of item representations (see also Ester et al. 2013), whereas changes in amplitude are associated with the allocation of attention resources to a limited number of items. An analogous explanation fits our findings, where the distributed changes in activity patterns associated with the demands placed on temporal individuation could reflect the precision of individuated representations, whereas the specific changes in amplitude reflected by RB could arise from processing limitations associated with the allocation of attentional resources that are necessary to bind an individuated representation (token) to its identity (type).

Decoding associated with the demands placed on temporal individuation was only attributed to a general effect of task difficulty in one ROI (the ACC), because the patterns of activity in the remaining ROIs did not discriminate between differences in reaction time. These remaining regions appear to reflect the demands associated with individuating two temporally distinct scenes, whereas the ACC appears to code for more general task-related effects. This latter finding fits well with the existing literature that suggests that the ACC is involved in general task conflict and cognitive control (Kerns et al. 2004).

Differences associated with temporal individuation were also distinguished from purely stimulus- or response-related effects, because classifiers could not consistently discriminate between repeated and nonrepeated stimuli (regardless of participants' responses) or responses (regardless of the physical stimulus presentation) in any of our "temporal individuation" regions. This finding suggests that these brain areas code for the interaction between stimulus and decision/response factors associated with successfully individuating two temporally distinct visual items. Of import, this stimulus-response interaction appears to be specifically related to temporal individuation in all regions with the possible exception of the bilateral LOC, since it was only in this area where patterns of activity could distinguish between miss and false alarm trials. These trials differ in stimulus and response characteristics but likely do not differ in the demands they place on temporal individuation. Moreover, when we collapsed decoding results across all ROIs for the hit vs. correct rejection comparison and miss vs. false alarm comparison, we found a significant overall difference between these two comparisons, suggesting that the information reflected by these two comparisons differs across the brain. In addition, signals associated with hits and correct rejections were restricted to brain regions that code for visual information or higher-level abstractions that do not depend on perceptual modality, and our decoding findings did not extend to other nonvisual (auditory) areas. Thus activity patterns associated with the differential demands placed on temporal individuation did not merely reflect false positives across the entire brain. Finally, our key individuation results cannot reflect general positive effects of target detection (e.g., reward, satisfaction), because both hits and correct rejections represent correct trials and would presumably have elicited the same level of reward and satisfaction.

In contrast to the wide set of brain areas that emerged in the current study, previous research and theoretical models of object individuation have attributed this operation to a single brain region (see Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007, 2009). Studies such as those by Xu and colleagues are common in cognitive neuroscience literature and assume that any given perceptual or cognitive process will be supported by a focal set of brain areas. Although this approach is hypothesis driven, it can be problematic as it limits the underlying neural substrates associated with particular processes and might miss the involvement of a more diffuse network of brain regions (see Vickery et al. 2011). For example, it was previously thought that signals associated with reward processes were represented in specific parts of the basal ganglia and prefrontal and parietal cortex (Elliott et al. 2000; Kable and Glimcher 2007; Kahnt et al. 2010; Rushworth and Behrens 2008; Vickery and Jiang 2009). More recently, however, Vickery et al. (2011) used MVPA to show that reward processes are reflected across the whole brain, suggesting that cognitive operations (such as temporal individuation, studied here) can be underpinned by an extensive neural network. Interestingly, these authors identified only a small subset of areas involved in reward processing when employing a univariate approach.

The widespread patterns of activity that emerged for temporal individuation are instead in line with existing accounts of consciousness, such as the "global neuronal workspace" model (Dehaene et al. 2003; Sergent and Dehaene 2004; see also Baars and Franklin 2003). According to this framework, conscious awareness is underpinned by a distributed network of "workspace neurons" that communicate via long-range connections in the brain. For a stimulus to be consciously perceived, it must activate this workspace, which then allows information to be accessed by a wide variety of processes. The global neuronal workspace model hypothesizes that these neurons are present in both early sensory areas and higher-level parietal and frontal areas, and information about a given stimulus is transferred through recurrent communications between different levels of the cortical hierarchy. In the context of the present study, these long-range connections provide a possible avenue in which lower and higher cortical areas interact during temporal individuation. We hypothesize that conditions in which it is more demanding to individuate two distinct object occurrences alter communications within this distributed workspace, leading to changes in the resulting patterns of activity in both lower- and higher-level brain areas. Our findings provide important insights into the neural underpinnings of temporal individuation in that we show it is a far more distributed process in the brain than initially proposed (e.g., Xu 2009; Xu and Chun 2009).

It is interesting to consider the discrepancy between the results we report presently and those from prior investigations into individuation by Xu and colleagues (Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007). These previous studies implicated the inferior IPS as the sole substrate of object individuation, which contrasts with the more diffuse group of brain regions we found in the current work. Even when we analyzed our data using the same univariate method as Xu and colleagues, we found that BOLD activity in a smaller group of ROIs was modulated by the demands placed on temporal individuation (ACC and superior medial frontal cortex, left hemisphere DLPFC and left hemisphere LOC, ts > 2.18, Ps $<$ .043, using the uncorrected test as in Xu and colleagues), but this subset did not include the inferior IPS. Below we consider several key differences between these previous studies and our work that could account for this discrepancy.

First is the episodic context in which object individuation was investigated. In our paradigm, items could only be individuated using temporal cues, whereas participants in Xu and colleagues' studies could only rely on the items' spatial locations (see Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007). It is unknown how the neural mechanisms associated with object individuation processes differ between the spatial and temporal domains, and the types of paradigms used in these studies and the present study are too dissimilar to make any strong conclusions regarding how these two operations might be related. Further research using a single paradigm that can manipulate spatial and temporal individuation processes will be useful in informing us about the nature of these two processes in the brain. Second, Xu and colleagues examined a different aspect of object individuation from the present study. In the present study we looked at the brain areas that support the process of individuation during perception, whereas Xu and colleagues' investigations focused on how individuated representations are consolidated, stored, and retrieved in visual short-term memory. An interesting possibility could be that different groups of brain areas are recruited when individuated representations are constructed during perception and later stored in memory.

Could the neural operation associated with temporal individuation simply reflect other forms of repetition processing in the brain? Repetition suppression, for instance, is a phenomenon wherein the presentation of a repeated stimulus leads to a reduction in neural activity (Desimone 1996; Grill-Spector et al. 2006; Henson and Rugg 2003; MacKay and Miller 1994). Like the distributed signals that emerged in response to the differential demands placed on temporal individuation, repetition suppression has also been detected extensively throughout the brain (Gotts et al. 2012). Our findings are unlikely to reflect repetition suppression for two key reasons, one reflecting methodology and the other a control analysis. First, the differential patterns of activity we observed for successfully individuating repeated and nonrepeated stimuli were present after gross differences in mean BOLD amplitude were removed from each condition. Thus the activity patterns that emerged for temporal individuation specifically reflect differences in spatial patterns of activity, not gross amplitude. Second, we were unable to decode purely stimulus-related changes in activity patterns associated with repeated and nonrepeated stimuli (hits and misses vs. correct rejections and false alarms) in any ROI. Rather, the regions that could discriminate between hits and correct rejections appear to be sensitive to the conditions under which the correct perceptual representation is successfully registered for a given stimulus. Our findings can therefore be distinguished from repetition suppression effects in the brain.

The present study also provides novel behavioral and fMRI evidence regarding the locus of RB. Although RB has been demonstrated for a variety of simple and complex stimuli (see, for a review, Coltheart 2010), our behavioral findings extend the generality of RB by providing the first evidence that this deficit can occur for the perception of scenes. In addition, our univariate fMRI results provide new insights into the ongoing debate over whether RB reflects an early (Kanwisher 1987; Luo and Caramazza 1996) or late (Fagot and Pashler 1995; Whittlesea and Masson 2005) processing locus. Although the limited electrophysiological investigations into RB suggest that this deficit arises between 220 and 350 ms after the repeated stimulus appears (Koivisto and Revonsuo 2008; Schendan et al. 1997), the paradigms used in these studies do not exclusively tap the capacity limits of individuation. To our knowledge, this study reflects the first neuroimaging work conducted using RB, where we found that the gross amplitude of BOLD activity in a higher-level premotor area involved in processes such as top-down attention and response selection (e.g., Marois et al. 2006; Schumacher et al. 2003) was influenced by whether participants successfully detected two repeated stimuli or not. Contrary to the prominent models of RB, this result suggests that this deficit has neither a purely perceptual or memory retrieval locus but reflects a mid-level top-down attentional bottleneck in conscious awareness (see also Chun 1997).

The direction of amplitude differences for the capacity limits of temporal individuation might appear counter to what one would predict, because activity in the left hemisphere premotor cortex was increased when a repetition was missed, compared with when it was correctly detected. Similar findings were noted in the AB literature, however, such that activity in two occipitotemporal regions were enhanced when two different letters were missed, relative to when they were detected (Kranczioch et al. 2005). Because RB is hypothesized to reflect an inability to bind an individuated token to a repeated type (Kanwisher 1987; Park and Kanwisher 1994), the enhanced activity associated with miss trials could reflect maintenance of the second target's type representation as the visual system attempts (but is unable) to register the source of this representation. Similar to Kanwisher's original type-token account (Kanwisher 1987; Park and Kanwisher 1994), this interpretation suggests that the increased activation that emerged for miss trials, relative to hit trials, reflects changes in processing of the second target rather than the first.

The present findings also add to the existing literature on the relationship between RB and other capacity-limited processes such as the AB. Behavioral comparisons between these two phenomena have found similar results to our lag RB experiment, in that they suggest that the AB and RB reflect distinct processing limitations (Chun 1997; Dux and Marois 2007). This apparent dissociation is further supported by the present fMRI findings, because we found different regions were implicated in RB relative to the AB, which has been associated with activity in parts of the lateral frontal, posterior parietal and occipitotemporal cortices (Kranczioch et al. 2005; Marcantoni

et al. 2003; Marois et al. 2004). Although we are limited in making strong conclusions about the possible neural dissociation between the AB and RB given that these investigations differed in paradigm and task, these findings do suggest that these two phenomena might be dissociable neurally as well as behaviorally. Our findings point towards the possibility of exploring the dissociation or overlap in the brain between different bottlenecks in conscious awareness.

We have provided the first evidence for an extensive set of brain regions that support the process of temporal individuation in perception, as well as the neural consequences associated with the processing limitations that lead to the RB deficit. We found that varying the demands placed on temporal individuation produced distributed changes in the patterns of activity across the brain, suggesting that such processes operate within a widespread neuronal workspace and involve multiple sources of information (e.g., stimulus, decisional, response). In contrast, when the capacity limit of individuation is reached, there are focal increases in the gross amplitude of BOLD activity, possibly reflecting changes in the allocation of attentional resources to processing the second repeated target. These findings highlight apparent differences in the neural coding of two distinct processes associated with temporal individuation, namely, the demands under which individuated representations are generated and the capacity limits that bottleneck the binding of these individuated tokens to an identity representation for conscious report.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

C.K.N. and P.E.D. conception and design of research; C.K.N. performed experiments; C.K.N., B.J.T.-R., and P.E.D. analyzed data; C.K.N., B.J.T.-R., and P.E.D. interpreted results of experiments; C.K.N. prepared figures; C.K.N. and P.E.D. drafted manuscript; C.K.N., B.J.T.-R., and P.E.D. edited and revised manuscript; C.K.N., B.J.T.-R., and P.E.D. approved final version of manuscript.

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APPENDIX B. DISTRIBUTED AND OVERLAPPING NEURAL SUBSTRATES FOR OBJECT INDIVIDUATION AND IDENTIFICATION IN VISUAL SHORT-TERM MEMORY

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Distributed and Overlapping Neural Substrates for Object Individuation and Identification in Visual Short-Term Memory

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Object individuation and identification are 2 key processes involved in representing visual information in short-term memory (VSTM). Individuation involves the use of spatial and temporal cues to register an object as a distinct perceptual event relative to other stimuli, whereas object identification involves extraction of featural and related conceptual properties of a stimulus. Together, individuation and identification provide the "what," "where," and "when" of visual perception. In the current study, we asked whether individuation and identification processes are underpinned by distinct neural substrates, and to what extent brain regions that reflect these 2 operations are consistent across encoding, maintenance, and retrieval stages of VSTM. We used functional magnetic resonance imaging to identify brain regions that represent the number of objects (individuation) and/or object features (identification) in an array. Using univariate and multivariate analyses, we found substantial overlap between these 2 operations in the brain. Moreover, we show that regions supporting individuation and identification vary across distinct stages of information processing. Our findings challenge influential models of multiple-object encoding in VSTM, which argue that individuation and identification are underpinned by a limited set of nonoverlapping brain regions.

Keywords: fMRI, multi-voxel pattern analysis, neural object file theory, object segmentation, visual short-term memory

Introduction

Many everyday activities, like searching for a stapler on a cluttered desk, rely on our ability to simultaneously isolate and identify multiple visual objects. To complete such a task, an observer must use spatial and temporal information to register each object as distinct (object individuation) and bind its features into a coherent form (object identification; Kahneman et al. 1992; Chun 1997; Pylyshyn 1989; Xu and Chun 2009). It is currently unclear how these processes are represented in the brain. In their "neural object file theory," Xu and Chun (2009) predict that the inferior intra-parietal sulcus (iIPS) plays a key role in object individuation, whereas the superior intra-parietal sulcus (sIPS) and lateral occipital complex (LOC) are involved in object identification (Xu 2007; Xu and Chun 2007; Xu 2008, 2009; Jeong and Xu 2013). Here, we test Xu and colleagues' prediction of a strict functional dissociation between the contributions of these and other regions to object individuation and object identification.

In a pioneering study, Xu (2009) provided evidence for dissociation between object individuation and identification within a single experiment. While undergoing functional magnetic resonance (fMRI) imaging, participants were briefly presented with a sample display consisting of 1 object, 4 identical objects, or 4 different objects (see Fig. 1). After a short delay, a single test item appeared centrally, and participants' task was to indicate whether the test identity matched 1 of the sample identities. Xu observed reduced blood-oxygen-level-dependent (BOLD) activity in the iIPS for 1-object displays, relative to both 4-identical-object and 4-different-object displays, which did not differ from each other. Conversely, the sIPS and LOC responded similarly for 1-object and 4-identical-object displays, but both had reduced BOLD activity relative to 4-different-object displays. Consistent with the neural object file theory (Xu and Chun 2009), these findings demonstrated that iIPS is sensitive to the number of objects in a display requiring individuation, whereas the sIPS and LOC respond to the number of distinct object identities requiring identification.

A potential shortcoming of Xu's (2009) study, and related empirical work (Jeong and Xu 2013; e.g., Xu 2007; Xu and Chun 2007; Xu 2008) upon which the neural object file theory is based, is that brain activity was analyzed within occipital and parietal regions only, thus potentially missing contributions from other brain regions. Further, these studies employed univariate analyses of the fMRI data, which are less sensitive to small changes in patterns of BOLD response that can emerge when activity is analyzed across groups of voxels (Haynes and Rees, 2006; Kamitani and Tong 2005). Our recent work using multi-voxel pattern analysis (MVPA) suggests that temporal individuation—registering objects as distinct perceptual events based on when they appear in "time"—recruits a broad set of frontal, parietal, and occipital regions (Naughtin et al. 2014). Based on this work, we predicted that such widespread networks of brain activity might also emerge from MVPA analyses of fMRI data obtained for displays in which objects must be individuated and identified in the "spatial" domain.

Previous work on the neural object file theory has been also limited to paradigms with short retention internals (Xu 2009), meaning that these studies have not been able to examine individuation and identification during distinct visual short-term memory (VSTM) stages. It is important to consider the role of different processing stages, given VSTM has been hypothesized to involve encoding, maintenance, and retrieval operations (e.g., Cohen et al. 1997; Courtney et al. 1997). Although Jeong and Xu (2013; also see Xu and Chun 2006) did use a long-delay VSTM paradigm and suggested that the iIPS, sIPS, and LOC are involved in individuation and identification processes during the encoding phase and beyond, their contrasts differed in both the number of objects presented and the number object identities. Thus, they could not unambiguously compare individuation and identification processes.

Here, we adopted a similar logic and approach to that used by Xu (2009), but with several important modifications, to test whether object individuation and identification can be

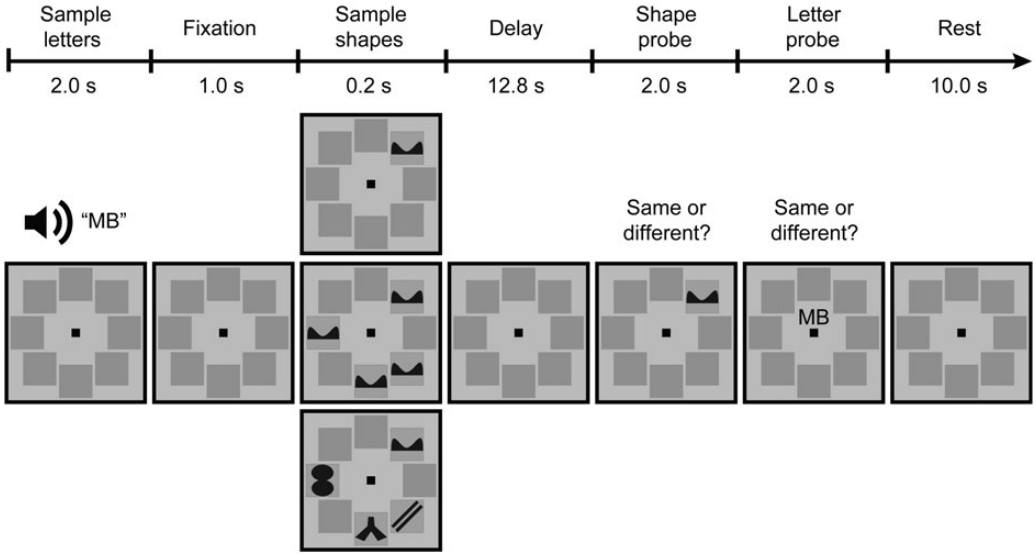

Figure 1. A schematic representation of the short-term memory paradigm. Each trial began with the auditory presentation of 2 letters, followed by a sample display consisting of 1 object, 4 identical objects, or 4 different objects. After an extended delay, observers identified whether a single test shape was the same as, or different from, 1 of the sample shapes, both in terms of its identity and location. The same judgment was also made for 2 subsequent test letters. The secondary auditory memory task was included to prevent participants from using verbal rehearsal strategies to remember the shape stimuli.

dissociated in the brain (as suggested in the neural object file theory, Xu 2009; Xu and Chun 2009). We analyzed activity across a broad set of brain regions using both univariate and MVPA approaches and compared the role of each region across encoding, maintenance, and retrieval stages of VSTM. In addition, unlike Xu's (2009) paradigm, our task required participants to remember both the identity *and* spatial location of all the objects in the display; this task ensured that both identification and individuation operations were engaged. By using both analytic approaches, we could first attempt to conceptually replicate the original univariate results from Xu (2009) under different task conditions and also determine whether other brain regions show evidence of object identification or individuation using the more sensitive MVPA approach.

Materials and Methods

Participants

We recruited 21 volunteers to participate in the experiment (12 females, mean age = 25.7 years, SD = 3.4 years). Data from 1 participant were excluded due to excessive head motion and from another due to a technical error that meant behavioral responses were not recorded. A post hoc power analysis confirmed that a minimum sample size of 10 was sufficient to have an 80% chance of detecting similar effects (Cohen's fs > 1.13) to those reported by Xu (2009). Participants had normal or corrected-to-normal vision, gave informed consent, and were financially reimbursed for their time ($15/h). The University of Queensland ethics committee approved the experimental protocol.

Design and Stimuli

Stimuli consisted of 8 distinct shapes derived from Xu and Chun (2006). Each shape was presented in black on a light gray background (3.1° × 3.1° of visual angle). Stimuli could appear in 1 of 8 dark gray placeholders (3.4° × 3.4°) arranged in a circular array, with each placeholder presented 5.3° from fixation. Placeholders were included to prevent grouping between closely presented objects (see Fig. 1; Xu 2009). The experiment was programed in MATLAB using the Psychophysics Toolbox (Brainard 1997; Pelli 1997).

Procedure

We used an STM paradigm, based on that of Xu (2009), to identify brain areas that selectively code for the number of objects (individuation) and/or number of object features (identification; see Fig. 1). This paradigm had 2 components: a primary VSTM task and a secondary verbal memory task. Each trial began with the auditory presentation of 2 letters via headphones, and participants were asked to rehearse these letters throughout the trial. The verbal memory task was included to prevent participants from using verbal rehearsal strategies for the visual stimuli (Todd and Marois 2004). After a brief interstimulus interval, a sample display consisting of 1 object, 4 identical objects, or 4 different objects was presented for 200 ms. Participants were instructed to remember the locations and identities of the sample objects during a subsequent 12.8-s retention interval. We used a slightly longer retention interval than is typically employed in slow event-related VSTM paradigms (e.g., see Harrison and Tong 2009; Serences et al. 2009; Emrich et al. 2013) to ensure that we could clearly distinguish between each stage of VSTM.

A single test shape appeared in 1 of the placeholders after the retention interval. The participants' task was to identify whether this test shape matched or mismatched 1 of the previously presented sample shapes, both in terms of its identity "and" location. It is important to note that a correct response on this task required that participants successfully individuate and identify each of the sample items, rather than merely their identity (cf. Xu and Chun 2007; Xu 2009, 2010; Jeong and Xu 2013). Thus, even though the 4-identical-object displays only contained a single identity, participants still had to individuate where each object appeared to produce a correct response. Two test letters were then presented, and participants made the same match/mismatch response for these letters, relative to the 2 sample letters presented at the beginning of the trial. Only response accuracy was emphasized, but participants had a fixed interval of 2 s in which to make each of their responses. The test shape and letter matched or mismatched 1 of the sample items an equal number of times.

Each trial was followed by a 12-s fixation period. This experimental design allowed us to isolate sources of BOLD activity previously associated with encoding, maintenance, and retrieval of the visual information (e.g., see Harrison and Tong 2009; Serences et al. 2009; Emrich et al. 2013). We chose these labels for the different time periods because previous studies have used them to describe the distinct phases of activity observed across long retention intervals. A more theoretically neutral approach might be to label the stages as "early," "middle," and "late," but we adopt the former set of labels to be

consistent with prior VSTM studies (e.g., Todd and Marois 2004; Xu and Chun 2006).

Participants completed 6 practice trials outside the scanner, followed by 8 scanning runs of 12 test trials. We only provided feedback for incorrect responses on practice trials, in which the central fixation square briefly turned red. Each run contained an equal number of trials per trial type. Trial types were presented in a randomized order, and the selection of stimuli and their locations were randomized across trials. Preliminary pilot testing ensured that participants could complete the task with a high level of accuracy (>80%). We made sure participants could perform this task well, as only correct trials were included in the fMRI analyses.

fMRI Acquisition

We acquired anatomical and functional images using a 3T Siemens Trio MRI scanner (Erlangen) and a 12-channel head coil. Participants laid supine in the scanner and viewed the visual display via a rear-projection mirror. Functional T2*-weighted images were acquired parallel to the AC–PC plane using a GRE EPI sequence (TR = 2 s, TE = 25 ms, FA = 90°, FOV = 192 × 192, matrix = 64 × 64, in-plane resolution = 3 × 3 mm). Each volume consisted of 33 slices with a thickness of 3 mm and a 0.3-mm inter-slice gap. In the middle of the session, we collected a T1-weighted anatomical image using an MPRAGE sequence (TR = 1.9 s, TE = 2.32 ms, FA = 9°, FOV = 192 × 230 × 256, resolution = 1 mm^3). We synchronized the stimulus presentation with the acquisition of functional volumes. Each run consisted of 184 volumes, including an 8-s dummy fixation block presented at the start of the run.

fMRI Analyses

We conducted preprocessing, univariate analyses, and MVPA with Brain Voyager QX 2.4 (Brain Innovation) and custom MATLAB code. We used both univariate and MVPA techniques to test for overall differences in BOLD amplitude and changes in the spatial patterns of activity across groups of voxels for each condition, respectively. There were 2 key comparisons of interest: First, to identify regions that reflect object individuation, we compared activity between displays containing 1 object and those containing 4 identical objects. Regions exclusively associated with this process should be sensitive to the episodic properties of objects (i.e., the number of objects in the display), but not to object identity (since this remained constant across the 2 display types). Second, to isolate regions that support object identification, we compared activity for displays containing 4 identical objects with those containing 4 different objects. If a given brain region specifically contributes to object identification, it should show a difference in activity in response to the number of distinct identities present, rather than to the number of objects per se. These were the same comparisons previously used by Xu (2009).

Preprocessing

Data preprocessing steps consisted of 3D motion correction (with all functional images aligned to the first image), slice-scan time correction, high-pass temporal filtering (3 cycles per run), and Talairach space transformation (Talairach and Tourmoux 1988). We did not apply spatial smoothing to the data to preserve fine-grained changes in activity for MVPA (as described in detail later).

Regions of Interest

All regions of interest (ROIs) were defined anatomically using mean Talairach coordinates from other relevant published studies. We used coordinates from Xu and Chun (2006) to define the iIPS, sIPS, and LOC, which have previously been implicated in object individuation and identification (e.g., Xu 2009; Xu and Chun 2009). To explore the role of other regions, we also isolated a set of frontal, parietal, and occipital regions involved in higher-level resource-limited processes such as response selection, decision making, and encoding (Szametitat et al. 2002; Heekeren et al. 2004; Dux et al. 2006; Dux et al. 2009; Tombu et al. 2011; Naughtin et al. 2014). Talairach coordinates for these regions were derived from our previous published studies (Dux et al. 2009; Naughtin et al. 2014). Since the sIPS and superior parietal lobule (SPL) ROIs overlapped in the majority of participants, we averaged the results across these 2 regions (referred to as sIPS/SPL).

Regions of interest were defined by a 11-mm^3 cube for the univariate analyses (we used the same number of voxels in each ROI as Xu 2009) and a 15-mm^3 or 21-mm^3 cube for MVPA. In both cases, the ROI cube was centered on the mean Talairach coordinates. We defined each ROI using a larger number of voxels for MVPA, compared with the univariate analyses, as it is conventional to use larger ROIs in the former to provide increased variability across voxels (e.g., Kamitani and Tong 2005; Harrison and Tong 2009; Gallivan et al. 2011; Oosterhof et al. 2012). As the sensitivity of MVPA depends upon the number of voxels included in the analysis, we used 2 different ROI sizes for MVPA—rather than choosing an arbitrary ROI size—to ensure the results were reliable, regardless of the number of voxels included in the classification analysis (Spiridon and Kanwisher 2002; Carp et al. 2011; Naughtin et al. 2014). For simplicity, we report the MVPA results from the 21-mm^3 ROIs that were significant across both ROI sizes. In addition to our main experimental ROIs, we also used the left and right primary auditory cortices as control regions (see also Naughtin et al. 2014). As these areas primarily respond to auditory information rather than visual information (e.g., pitch; Hyde et al. 2008), they should not show any evidence of individuation or identification. The auditory cortex control regions were defined in the same way as the other ROIs, with the ROI cube centered on the superior portion of the temporal lobe (Rademacher et al. 2001).

Univariate Analysis

The purpose of the univariate analysis was to identify gross changes in BOLD amplitude that have been hypothesized to reflect the processes of individuation or identification. We extracted time courses for each display condition with percentage signal change at each time point calculated relative 1 volume prior to trial onset. This procedure was performed separately for each ROI and participant. To determine the peak amplitude for encoding, maintenance, and retrieval, we collapsed time courses across all display types, participants, and ROIs and selected the 2 volumes corresponding to the peak at each stage. The time windows for the encoding, maintenance, and retrieval stages of VSTM were 4–8 s, 12–16 s, and 18–22 s after sample display onset, respectively (similar to previous VSTM studies, Todd and Marois 2004; Xu and Chun 2006; Jeong and Xu 2013).

Multivariate Analyses

Multi-voxel pattern analysis was employed to assess for individuation- or identification-related changes in activity that may be present in the ensemble patterns of activity of each ROI (Kamitani and Tong 2005; Haynes and Rees 2006). This type of approach is more sensitive to small, reliable changes in activity that might not be detected in standard univariate analyses. We used custom MATLAB software and a linear support vector machine algorithm (Chang and Lin 2011) for these analyses. We ran separate classification analyses for encoding, maintenance, and retrieval stages for each ROI; data for each voxel were averaged across the respective time windows (4–8, 12–16, and 18–22 s after sample display onset). Prior to MVPA, these data samples were transformed into z-scores and mean-centered to remove any amplitude differences between conditions (Esterman et al. 2009; Tamber-Rosenau et al. 2011). To assess classification performance, we used the leave-one-out cross-validation procedure. On each loop, 1 run was reserved to test the classifier's generalization performance and the remaining 7 runs were used to train the classifier. We averaged classification performance for each ROI across all cross-validation loops and compared this accuracy with chance performance (50%) using a 1-sample *t*-test ($P < 0.05$, Bonferroni-corrected for the number of ROIs and number of VSTM stages tested).

Results

Behavioral Performance

Performance on the verbal memory task did not differ between the 3 display types (88.7–90.6% accuracy across all display

types; $F < 1$), which is consistent with the idea that auditory and VSTM systems operate independently of each other (Baddeley 1992; Smith and Jonides 1998). We used Cowan's K formula (Cowan 2001) to estimate participants' VSTM capacity for each display type in the visual memory task. As shown in Figure 2, K estimates significantly differed across display types, $F_{2,36} = 75.21$, $P < 0.001$, $\eta_F^2 = 0.81$. Behavioral performance was close to ceiling for 1 object and 4 identical objects, but participants could only hold about 2 objects in memory for the 4-different-object displays.

Univariate Analyses

We first tested for gross differences in BOLD amplitude associated with individuation and identification processes. For each comparison, we conducted a repeated-measures analysis of variance with factors of display type (1 object, 4 identical objects, and 4 different objects) and stage (encoding, maintenance, and retrieval), separately for each ROI. A significant main effect of display type indicates that a given region is consistently modulated by 1 or both of the processes of interest (i.e., the number of objects—"individuation"; or the number of object features—"identification") and a significant display type by stage interaction signals that activity associated with the process(es) of interest varies across different VSTM stages. Whenever the analysis for a given region yielded a significant interaction, we ran follow-up t-tests at each VSTM stage to identify the stage(s) at which that region was recruited for the process(es). We present results from the significant regions according to whether they were modulated by the number of objects, the number of object features, or both.

Individuation-Related Activity

Areas associated with object individuation showed either an overall amplitude difference between 1-object versus 4-identical-object displays or an interaction between these 2 display types and stage (see Fig. 3). We found that the left and right iIPS were showed a significant main effect of display type, $Fs_{2,36} > 4.44$, $Ps < 0.024$, $\eta_P^2 s > 0.20$, and follow-up t-tests revealed that activity was significantly reduced for displays with 1-object, compared with 4-identical-object displays, $ts_{18} > 2.95$, $Ps < 0.009$. The comparison between 4 identical objects and 4 different objects was not significant, $ts_{18} < 1.08$, $Ps > 0.294$. Consistent with previous work by Xu (2009), we found a profile in the univariate activity that suggests that the iIPS is recruited for object individuation and not object identification. Here, we also show, for the first time, that the involvement of these regions in individuation is consistent across all 3 VSTM stages.

Identification-Related Activity

We identified areas that support object identification as those for which there were significant amplitude differences between 4-identical-object displays and 4-different-object displays, or an interaction between these 2 display types and stage (see Fig. 4). The bilateral anterior cingulate cortex (ACC) and the right dorsolateral prefrontal cortex (DLPFC) showed a significant main effect of display type, $Fs_{2,36} > 3.62$, $Ps < 0.040$, $\eta_P^2 s > 0.17$. Follow-up t-tests revealed that this effect was driven by an enhanced response for 4 different objects versus 4 identical objects, $ts_{18} > 2.40$, $Ps < 0.027$.

Five additional ROIs showed a significant display type × stage interaction, $Fs_{4,72} > 2.87$, $Ps < 0.047$, $\eta_F^S s > 0.14$ (4 of which also showed a significant effect of display type, $Fs_{2,36} > 5.14$, $Ps < 0.011$, $\eta_F^S s > 0.22$): superior medial frontal cortex (SMFC), right premotor cortex (PMC), bilateral insula, and left inferior frontal junction (IFJ). All these regions showed a significant difference in activity between 4 identical and 4 different objects for the encoding and maintenance time windows, $ts_{18} > 2.06$, $Ps < 0.054$, and the right insula also showed a

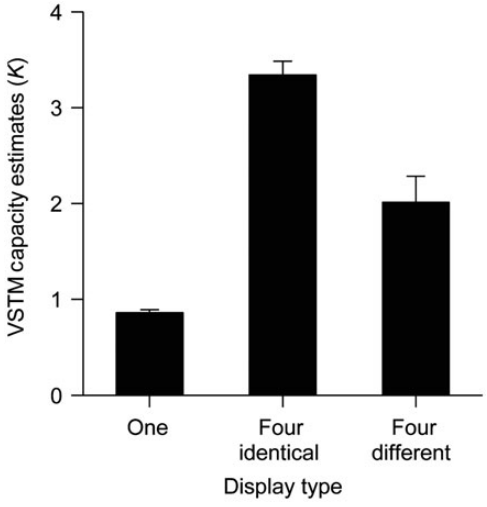

Figure 2. Behavioral estimates of VSTM capacity as a function of the 3 display types. These estimates were calculated using Cowan's (2001) K formula. Error bars denote standard error of the mean.

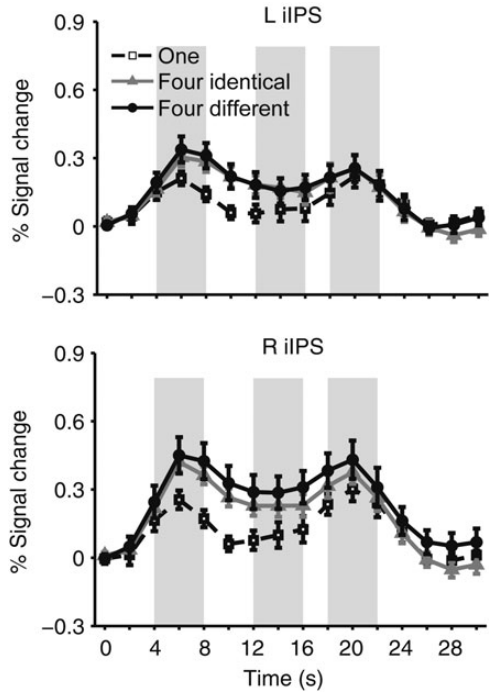

Figure 3. BOLD time courses during encoding, maintenance, and retrieval stages for regions that were influenced by the number of objects in the display (reflecting object individuation). These areas showed a significant difference between 1-object and 4-identical-object displays at 1 or more VSTM stages. Separate lines denote display types, and the shaded gray areas reflect the time window used for each stage of VSTM. Error bars denote standard error of the mean.

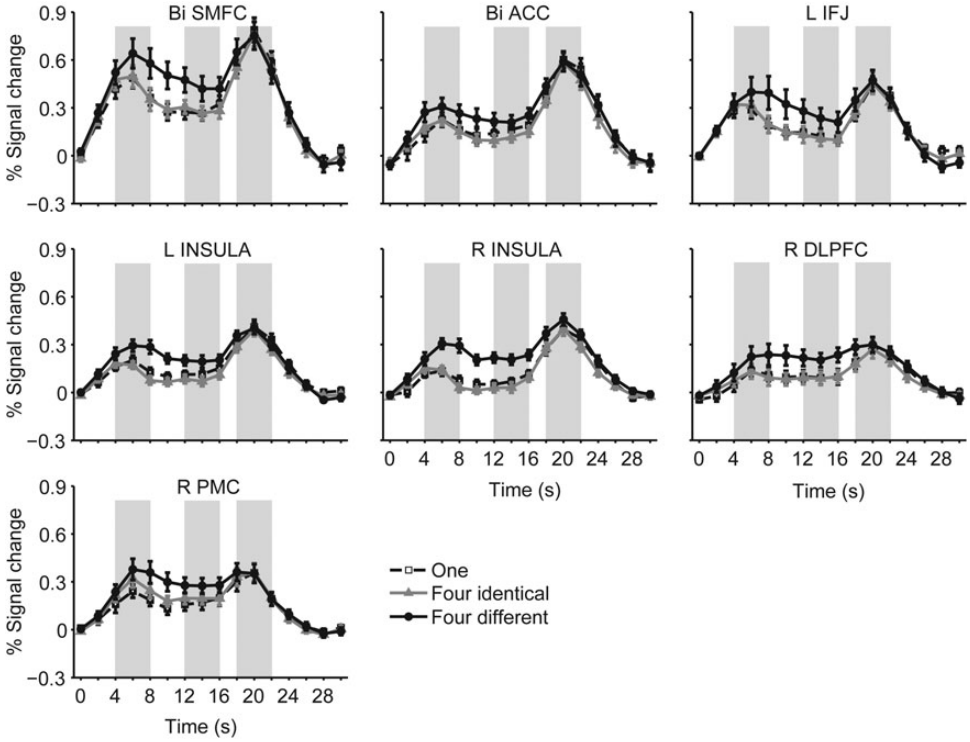

Figure 4. BOLD time courses during encoding, maintenance, and retrieval periods for regions that were influenced by the number of object features in the display (reflecting object identification). These regions showed a significant difference between displays containing 4 identical objects and those with 4 different objects at 1 or more VSTM stages. Separate lines denote display types, and the shaded gray areas reflect the time window used for each stage of VSTM. Error bars denote standard error of the mean.

significant difference at retrieval, $t_{18} = 3.17$, $P = 0.005$. Unlike the individuation results, in a task where both identity and location information had to be processed, we failed to observe Xu's (2009) finding that object identification is restricted to the sIPS and LOC. Instead, we found a different set of brain regions was associated with this process, and these regions were active during the encoding and maintenance time windows.

Individuation- and Identification-Related Activity

In addition to those regions that were modulated either by the number of objects (individuation) or object features (identification), we also found some regions that showed evidence of *both* processes: left PMC, right IFJ, and bilateral sIPS/SPL (see Fig. 5). These 4 regions showed a significant interaction between display type and stage, $Fs_{4,72} > 4.09$, $Ps < 0.005$, $\eta_F^2 s > 0.19$. Follow-up *t*-tests revealed that all regions showed a difference between 1 object and 4 identical objects at encoding, $ts_{18} > 2.01$, $Ps < 0.059$. A significant difference between 1-object and 4-identical-objects displays was also observed during maintenance in the bilateral sIPS/SPL regions, $ts_{18} > 2.15$, $Ps < 0.045$, and in the right hemisphere sIPS/SPL during retrieval, $t_{18} = 2.66$, $P = 0.016$. For the identification comparison, activity was significantly reduced for 4-identical-object displays versus 4-different-object displays for the left PMC, right IFJ, and bilateral sIPS/SPL during encoding and maintenance, $ts_{18} > 2.11$, $Ps < 0.049$. Contrary to what Xu and Chun originally proposed (Xu 2009; Xu and Chun 2009), these findings suggest that individuation and identification cannot be completely dissociated in the brain under conditions where identity and location must be analyzed, as our univariate results revealed a subset of brain areas that are involved in *both* operations.

Multivariate Analyses

Similar to the univariate analyses, we conducted MVPA on data corresponding to encoding, maintenance, and retrieval stages of VSTM. In separate analyses, we trained a classifier to discriminate between the same 2 key comparisons used in the univariate analyses: 1 object versus 4 identical objects for individuation, and 4 identical objects versus 4 different objects for identification. Classification performance for each ROI was compared with chance (50%) using a one-sample *t*-test and a significance threshold of $P < 0.05$, Bonferroni-corrected for the 18 regions tested (i.e., 16 main regions of interest plus 2 control regions) and the 3 VSTM stages (critical $P = 0.0009$).

Compared with the univariate analyses, the MVPA approach revealed a more extensive neural overlap between individuation and identification processes (see Fig. 6). Six regions displayed evidence of either individuation or identification processes. Specifically, right IFJ, bilateral insula, and left LOC showed significant decoding for the number of objects ($ts_{18} > 4.47$, $Ps < 0.016$ [corrected]), whereas the right DLPFC showed significant decoding for the number of object features ($t_{18} = 4.78$, $P = 0.008$ [corrected]). For 9 of the sixteen regions—the left IFJ, left sIPS/SPL, left LOC, ACC, SMFC, and bilaterally in the PMC and iIPS—classifiers could decode activity between the "number of objects" comparison (1 object vs. 4 identical objects) and the "number of object features" comparison (4 identical vs. 4 different objects) in 1 or more VSTM stages, $ts_{18} > 4.06$, $Ps < 0.040$ (corrected). Of key interest, we found that activity in the bilateral iIPS, left sIPS/SPL, and left LOC

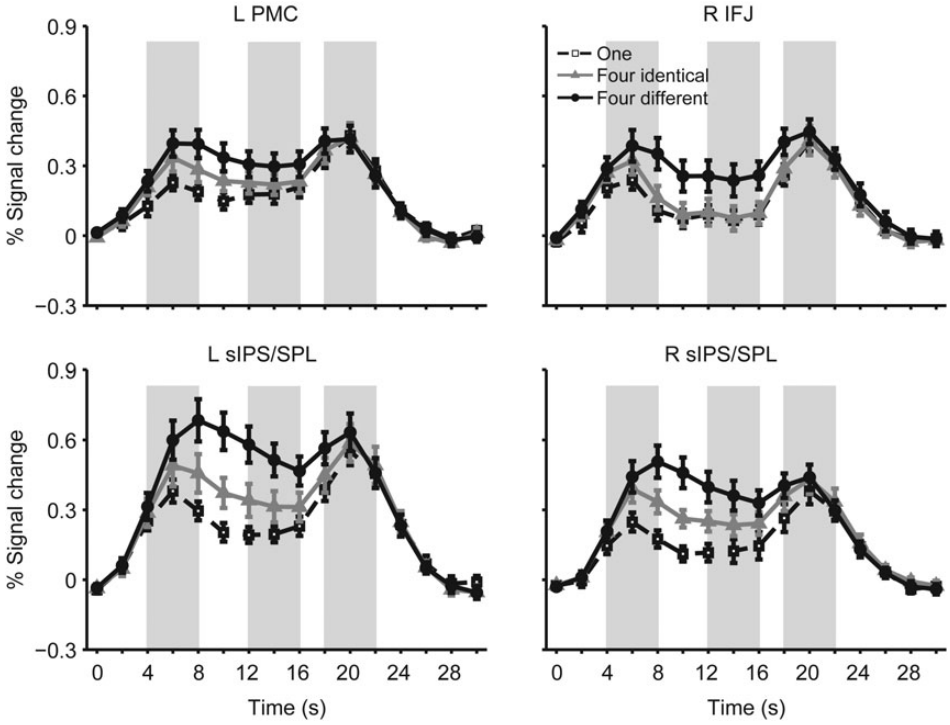

Figure 5. BOLD time courses during encoding, maintenance, and retrieval periods for regions that were influenced by both the number of objects (object individuation) and number of object features (object identification). These regions showed significant differences between both comparisons of interest at 1 or more VSTM stages. Separate lines denote display types, and the shaded gray areas reflect the time window used for each stage of VSTM. Error bars denote standard error of the mean.

could be decoded for the 2 comparisons of interest at single or multiple stages of VSTM, suggesting these regions represent "both" individuation and identification processes, rather than 1 distinct process. In addition, while activity associated with the number of objects or object features could be decoded across all VSTM stages in some regions (e.g., bilateral sIPS/SPL, left PMC, and right LOC), other brain areas were recruited during specific stages (e.g., within the left IFJ, the number of object features presented could be decoded during encoding and maintenance, but the number of objects per se could be decoded at retrieval only).

Taken together, these findings suggest an extensive interplay between object individuation and identification in the brain and suggest that signals associated with these processes can be detected across a wide network of regions at each stage of VSTM (see also Naughtin et al. 2014). These findings are inconsistent with the neural object file theory put forward by Xu and Chun (2009), which predicts that individuation and identification are subserved by a limited set of nonoverlapping brain regions. Rather, we show that activity is modulated in a distributed set of common regions when observers are required to identify and individuate a set of items in a display (novel conditions that are not accounted for in the current conceptualization of the neural object file theory).

One caveat to these conclusions is that the differences we observed for individuation and identification could instead reflect some general, unspecified effect of task difficulty. As we elaborate on in the section General Discussion, such task difficulty effects are a potential issue for any study where there are behavioral differences between conditions (including the previous work by Xu and colleagues). It is therefore challenging to operationalize general, unspecified effects of task difficulty as a measure that is independent of the manipulated factors. Nevertheless, as MVPA has the potential to exacerbate such difficulty effects (e.g., see Todd et al. 2013), we addressed this issue by balancing reaction times across our 2 key comparisons of interest. Prior to conducting the MVPAs, we equated reaction times between the "number of objects" and "number of object features" comparisons by removing the slowest trials from the condition with the longest average reaction time and the fastest trials from the condition with the shortest average reaction time, until there was no significant reaction time difference between the conditions, $ts_{14} < 1.56$, $Ps > 0.141$. Data from 4 participants were removed from these analyses, as we could not balance their reaction times between conditions for 1 or both comparisons (leaving the sample at $n = 15$).

Despite the substantial reduction in power due to fewer trials and subjects included in this analysis, we found 32 of our original 43 significant decoding effects held once reaction time was equated (see Table 1). The number of objects and/or object features could no longer be discriminated in the maintenance or retrieval periods for the left IFJ, right DLPFC, bilateral PMC, left insula, and right sIPS/SPL ($Ps > 0.05$, corrected, across 1 or both ROI sizes). For the encoding period, the number of objects in the right LOC and the number of object features in the left PMC could not be reliably discriminated ($Ps > 0.05$, corrected, across 1 or both ROI sizes). It is possible that those effects that were no longer reliable in the reaction time-balanced analysis might have reflected some general effect of task difficulty, rather than the processes of interest. An alternative explanation is that this control analysis simply had less power than the main analysis to detect these effects, due to the reduction in trial numbers and subjects. Although these reaction time-controlled results raise a degree of doubt about

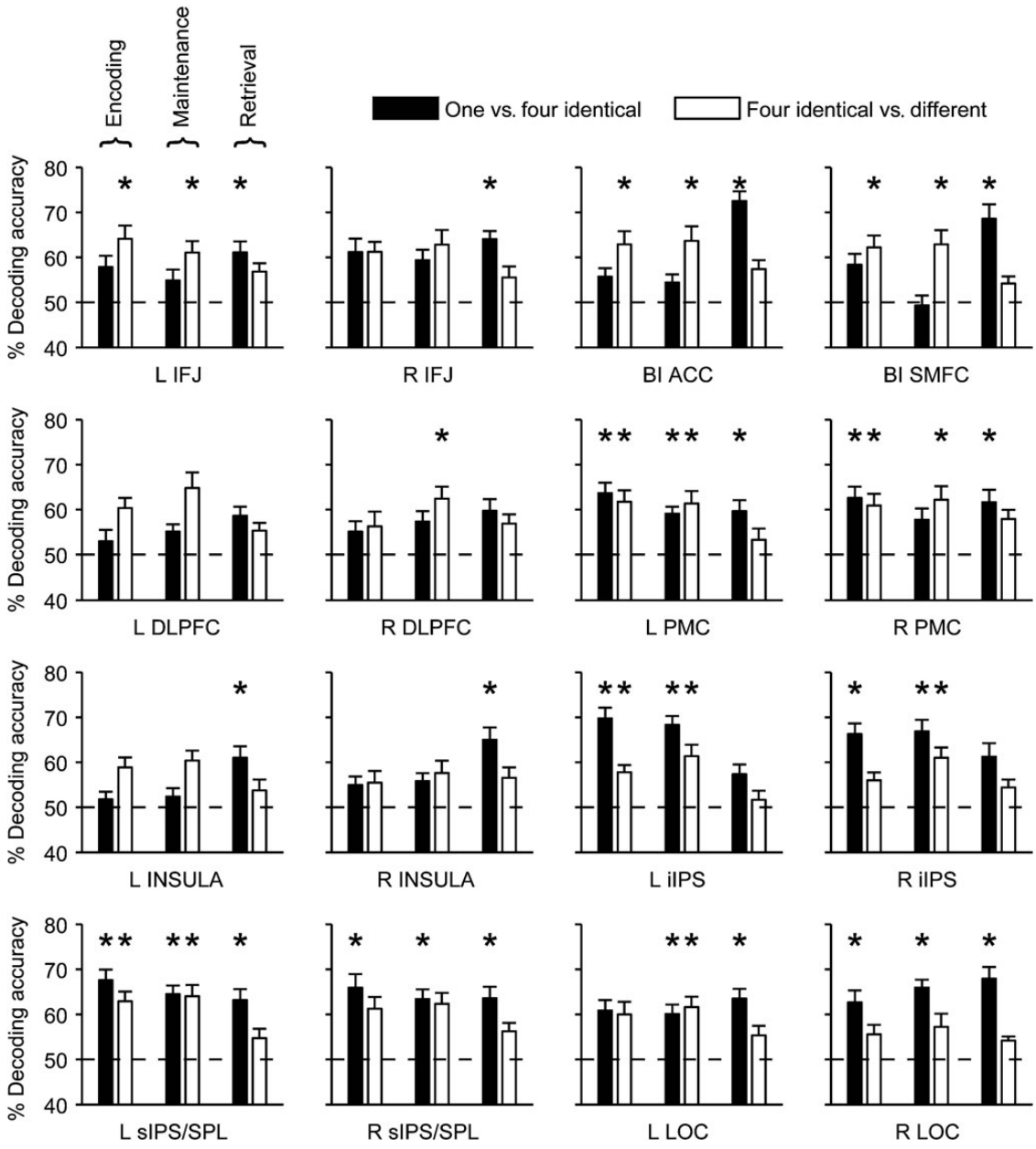

Figure 6. Mean classification performance during encoding, maintenance, and retrieval periods across all key regions of interest. Classifiers were trained to discriminate between the 2 key comparisons: 1 object versus 4 identical objects ("number of objects" comparison; object individuation), and 4 identical objects versus 4 different objects ("number of object features" comparison; object identification). Results from each region are displayed on separate plots. Asterisks denote classification performance that is significantly greater than chance across both ROI sizes (Bonferroni-corrected for the number of regions and VSTM stages tested). Error bars reflect standard error of the mean.

the role played by some of our ROIs in individuation and identification, the overall results were largely robust to this balancing procedure. Collectively, our findings demonstrate that individuation and identification processes can be detected in overlapping substrates that are distributed across the brain.

Control Analysis

We conducted the same MVPA using data from 2 control regions (left and right auditory cortices) that should not be involved in visual individuation or identification. The purpose of this control analysis was to ensure that the decoding differences described earlier reflect the processes of interest—object individuation and identification—rather than any unanticipated artifact of our data, task design, or analyses. As expected, classifiers could not reliably discriminate between the number of objects in the display (1 object vs. 4 identical objects) and the number of object features (4 identical objects vs. 4 different objects) in the left or right auditory cortices at any VSTM stage, $ts_{18} = 2.64$, $Ps > 0.855$ (corrected). These control results confirm that the observed differences between the display types within the experimental ROIs reflect processes specifically associated with individuating or identifying multiple objects.

General Discussion

The purpose of the current study was twofold: We wanted to test whether object individuation and identification are distinct processes in the brain and whether the brain regions that

Table 1

Mean classification performance during encoding, maintenance, and retrieval periods for the main decoding analysis (where reaction time [RT] was not equated) and the task difficulty control analysis (where RT was equated)

Region of interest	VSTM: encoding		VSTM: maintenance		VSTM: retrieval	
	Unequal RTs	Equal RTs	Unequal RTs	Equal RTs	Unequal RTs	Equal RTs
IFJ (L)						
1 vs. 4I	57.8 (11)	56.1 (11)	54.9 (10)	56.1 (12)	61.1 (10)*	59.5 (9)
4I vs. 4D	64.1 (12)*	68.8 (15)*	61.1 (11)*	62.9 (12)	56.8 (8)	61.5 (12)
IFJ (R)						
1 vs. 4I	61.2 (13)	60.3 (15)	59.4 (10)	59.5 (12)	64.0 (8)*	63.2 (9)*
4I vs. 4D	61.2 (9)	62.1 (12)	62.8 (14)	63.8 (15)	55.6 (10)	64.7 (15)#
ACC (Bi)						
1 vs. 4I	55.7 (8)	55.4 (10)	54.4 (8)	55.2 (10)	72.5 (9)*	73.3 (9)*
4I vs. 4D	62.9 (12)*	67.0 (15)*	63.6 (14)*	66.8 (15)*	57.4 (9)	73.1 (11)*
SMFC (Bi)						
1 vs. 4I	58.3 (10)	60.0 (12)	49.4 (9)	52.8 (11)	68.6 (14)*	69.2 (12)*
4I vs. 4D	62.2 (11)*	67.2 (9)*	62.9 (13)*	66.6 (13)*	54.2 (7)	67.6 (13)
DLPFC (L)						
1 vs. 4I	52.9 (11)	54.5 (11)	55.1 (7)	56.9 (11)	58.6 (8)	55.1 (8)
4I vs. 4D	60.3 (10)	62.6 (14)	64.8 (15)	64.9 (15)	55.3 (8)	60.3 (12)
DLPFC (R)						
1 vs. 4I	55.1 (10)	55.5 (11)	57.3 (10)	58.2 (11)	59.7 (11)	60.1 (12)
4I vs. 4D	56.3 (14)	60.3 (14)	62.4 (11)*	65.2 (13)	56.9 (9)	60.7 (10)*
PMC (L)						
1 vs. 4I	63.6 (10)*	66.1 (12)*	59.1 (6)*	61.4 (10)	59.7 (10)*	59.7 (11)
4I vs. 4D	61.7 (11)*	61.4 (11)	61.3 (12)*	62.5 (12)	53.3 (11)	62.3 (14)
PMC (R)						
1 vs. 4I	62.6 (11)*	63.7 (9)*	57.7 (11)	57.9 (13)	61.7 (12)*	58.5 (14)
4I vs. 4D	60.9 (11)*	64.8 (13)*	62.2 (13)*	64.0 (14)#	57.9 (9)	62.1 (11)
Insula (L)						
1 vs. 4I	51.8 (7)	52.3 (12)	52.4 (8)	54.3 (10)	61.0 (11)*	59.2 (10)
4I vs. 4D	58.9 (9)	61.7 (12)	60.4 (9)	63.8 (10)	53.7 (10)	59.5 (14)
Insula (R)						
1 vs. 4I	55.0 (8)	54.7 (9)	55.8 (7)	56.9 (10)	65.0 (11)*	63.9 (13)#
4I vs. 4D	55.5 (11)	60.3 (16)	57.6 (11)	62.8 (11)*	56.6 (10)	63.0 (12)*
iIPS (L)						
1 vs. 4I	69.8 (10)*	66.2 (12)*	68.3 (8)*	67.2 (9)*	57.3 (9)	57.4 (7)
4I vs. 4D	57.8 (7)*	67.2 (13)*	61.3 (11)*	65.3 (12)*	51.6 (9)	59.8 (14)
iIPS (R)						
1 vs. 4I	66.3 (10)*	65.1 (12)*	66.9 (11)*	69.7 (12)*	61.2 (13)	59.4 (13)
4I vs. 4D	56.0 (7)	65.3 (14)*	61.0 (10)*	66.9 (11)*	54.4 (7)	59.0 (12)
sIPS/SPL (L)						
1 vs. 4I	67.6 (10)*	67.4 (10)*	64.5 (8)*	63.7 (10)*	63.2 (10)*	61.8 (11)*
4I vs. 4D	62.9 (9)*	68.7 (11)*	64.0 (10)*	66.5 (12)*	54.8 (9)	67.0 (10)*
sIPS/SPL (R)						
1 vs. 4I	66.0 (13)*	66.7 (13)*	63.4 (9)*	65.1 (10)*	63.6 (11)*	62.7 (12)
4I vs. 4D	61.3 (11)	67.0 (14)*	62.3 (10)	66.6 (12)*	56.2 (8)	63.6 (11)*
LOC (L)						
1 vs. 4I	60.9 (10)	62.4 (10)*	60.1 (9)*	62.8 (8)*	63.5 (9)*	62.2 (11)*
4I vs. 4D	60.0 (12)	64.8 (14)	61.6 (10)*	67.6 (11)*	55.4 (9)	60.6 (13)
LOC (R)						
1 vs. 4I	62.7 (11)*	60.1 (12)	66.0 (7)*	66.7 (6)*	67.9 (11)*	67.5 (12)*
4I vs. 4D	55.6 (9)	61.2 (12)	57.2 (13)	58.0 (11)	54.2 (4)	68.8 (11)*

Note: Standard deviations are denoted in the parentheses. Decoding accuracies for each region are displayed separately for the "number of objects" comparison (1 object vs. 4 identical objects [1 vs. 4I]) and the "number of object features" comparison (4 identical objects vs. 4 different objects [4I vs. 4D]). All statistical results are Bonferroni-corrected for the number of regions and VSTM stages tested. *$P < 0.050$, #$P < 0.082$ (marginally significant).

support these operations vary across different processing stages of VSTM. Using the same logic and a similar experimental approach to that previously employed by Xu (2009), we compared changes in BOLD activity under conditions that differed in either the number of objects (1 object vs. 4 identical objects) or the number of object features (4 identical objects vs. 4 different objects). We used a slow event-related protocol that allowed us to separate activity reflected by encoding, maintenance, and retrieval VSTM stages. Across both univariate analyses and MVPA, we found evidence for both distinct and overlapping neural substrates for individuation and identification. The overlap between these 2 operations was most apparent in the MVPA results, where 9 ROIs showed evidence of individuation and identification at a single or multiple VSTM stages. These results suggest that individuation and identification have distributed and overlapping neural substrates (see also Naughtin et al. 2014), and these operations are not restricted to a few process-specific brain areas, as has previously been suggested (Xu 2009; Xu and Chun 2009).

The involvement of most brain regions in individuation and identification was variable across VSTM stages, particularly at retrieval. The timing of the auditory memory response, however, could account for the absence of individuation- or identification-related activity at the retrieval stage. In other words, activity associated with the auditory memory response could have obscured effects present in the visual memory response. By contrast, the observed modulations associated with differences in number of objects or object features in the display could not simply reflect an artifact of our data, task design, or analysis, as these same comparisons yielded no significant decoding in 2 auditory control regions.

One could argue that data from our main analyses do not rule out the potential confound of general, unspecified task difficulty. In fact, such difficulty effects are also a possible issue for the prior studies by Xu and colleagues, and likely any other study in cognitive neuroscience where performance differs between conditions (e.g., the standard parametric manipulation). Similarly, it is equally problematic to interpret imaging findings when there is no behavioral difference between conditions. Here, we find complementary differences in behavior and the brain. In an attempt to rule out the potential confound of task difficulty, we equated reaction times between our 2 key comparisons, and the results were largely comparable with those from our main decoding analysis. We still found activity in a distributed set of brain regions that was specifically associated with individuation or identification, and 7 of the original 9 regions showed evidence of both processes (ACC, SMFC, right PMC, bilateral iIPS, left sIPS/SPL, and left LOC). Thus, any nonspecific effect of difficulty does not appear to account for the overlap between individuation and identification that we observe.

The large number of common brain regions associated with individuation and identification, either at the same stage or different stages of VSTM, contrasts with theoretical accounts and fMRI results put forward by Xu and colleagues (Xu and Chun 2006, 2007, 2009; Xu 2009; Jeong and Xu 2013). For example, Xu (2009) used univariate analyses and found evidence for individuation tapping only the iIPS and identification only the sIPS and LOC. Within these 3 posterior regions, however, we found the greatest overlap between individuation and identification, particularly during encoding and maintenance stages of VSTM. These discrepant findings resonate with seminal MVPA work by Haxby et al. (2001), who found that decoding techniques, unlike univariate analyses, reveal overlapping stimulus representations in the ventral temporal cortex, even though this cortical area was previously thought to contain subregions that only responded to a single stimulus category (i.e., faces and man-made objects such as houses, scissors, and chairs). Thus, it appears that information pertaining to individuation and identification is reflected by more subtle changes in BOLD activity, which we were able to detect using MVPA.

There are several other reasons why Xu and colleagues might not have observed an overlap between individuation and identification. First, in the present study, participants were required to individuate and identify "each item" within the sample display. By contrast, Xu (2009) had participants judge a test shape based upon its identity only, and not its location. The active involvement of each process in completing the task could have enhanced neural responses associated with individuation and identification. While we cannot say whether the same overlap between object individuation and identification would be observed if we used a pure identification task (e.g., Xu 2009), our findings do suggest that these processes are reflected in common neural substrates in tasks that require participants to individuate and identify all objects in the display.

Second, we used a longer memory retention period. Xu (2009) had participants maintain sample shapes in memory for only 1 s, and thus, activity associated with each VSTM stage was collapsed and finer differences at any given stage could have been temporally smeared. Finally, we analyzed activity in a wider set of ROIs. This broader approach ensured a more thorough exploration of individuation and identification processes in the brain and revealed that signals associated with each of these processes can be detected in a far more distributed neural network.

Results from our recent fMRI study on "temporal" individuation (Naughtin et al. 2014) are consistent with the current findings of involvement of both lower-level perceptual regions and higher-level executive regions in spatial individuation and identification processes. In the previous study, we used a repetition blindness paradigm in which participants had to detect the presence of a scene repetition embedded within a rapid stream of distractors. As participants are typically poorer at individuating an item when it is preceded by one with the same identity (Kanwisher 1987; Park and Kanwisher 1994), we hypothesized that it would be more demanding to successfully individuate 2 temporally distinct scenes when they had the same identity (repeated), relative to different identities (nonrepeated). Using MVPA, we found that activity in the same set of lower- and higher-level regions could discriminate between correctly identified repeated and nonrepeated scenes. Thus, even though our previous investigation (Naughtin et al. 2014) and the current study employed paradigms that differed in both task demands and stimulus properties, findings from both point to a common distributed network for identification and individuation in the spatial and temporal domains.

We are not the first to propose a distributed neural network as the underlying neural basis for perceptual or cognitive abilities. For example, in their MVPA study, Vickery et al. (2011) found that reward processes are reflected across many brain regions, yet a smaller, more focal set of regions emerged in the univariate analysis. In addition, Duncan (2010, 2013) has proposed that a large range of cognitive tasks are underpinned by a distributed set of frontal and parietal regions, which he refers to as the "multiple demands" system. These findings underscore the importance of exploring the role of distributed brain regions in any given perceptual or cognitive process.

Conclusion

The present evidence challenges an earlier view that object individuation and identification are subserved by a relatively small set of distinct brain regions (as suggested by Xu 2009; Xu and Chun 2009). Both univariate analyses and MVPA suggested that individuation and identification are instead reflected across a larger group of brain regions and that these processes have overlapping neural substrates. We propose that individuation and identification might operate within a distributed neural network in which lower- and higher-level regions communicate. Our findings further indicate that earlier work on the neural bases of object individuation and identification may have been restricted by the number of regions tested and the sensitivity of the data analysis techniques employed. At the very least, our data illustrate conditions in which the neural object file theory (Xu and Chun 2009) cannot account for how object individuation and identification are represented in the brain, that is, when the observer must track both the location and identity of objects. Furthermore, we found involvement of these distributed regions varied across different processing stages of VSTM, in a substantial proportion of regions. These results provide new insights into the nature of the neural substrates that give rise to individuation and identification—2 operations that are crucial for a stimulus to reach conscious awareness and be consolidated in VSTM.

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Notes

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